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REVIEW AND SYNTHESIS

Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences

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Abstract

Myriad tiny insect species take to the air to engage in windborne migration, but entomology also has its “charismatic megafauna” of butterflies, large moths, dragonflies and locusts. The spectacular migrations of large day-flying insects have long fascinated humankind, and since the advent of radar entomology much has been revealed about high-altitude night-time insect migrations. Over the last decade there have been significant advances in insect migration research, which we review here. In particular, we highlight: (i) notable improvements in our understanding of lepidopteran navigation strategies including the hitherto unsuspected capabilities of high-altitude migrants to select favourable winds and orientate adaptively; (ii) progress in unravelling the neuronal mechanisms underlying sun compass orientation and in identifying the genetic complex underpinning key traits associated with migration behaviour and performance in the monarch butterfly; and (iii) improvements in our knowledge of the multifaceted interactions between disease agents and insect migrants, in terms of direct effects on migration success and pathogen spread, and indirect effects on the evolution of migratory systems. We conclude by highlighting the progress that can be made through inter-phyla comparisons, and identify future research areas that will enhance our understanding of insect migration strategies within an eco-evolutionary perspective.

Keywords

Autographa gamma, flight orientation, insect diseases, locusts, monarch butterfly, *Pantala flavescens*, radar entomology, *Spodoptera exempta*, trade-offs, *Vanessa cardui*.

INTRODUCTION

Migratory species comprise a significant proportion of all major lineages of the animal kingdom, with species undertaking journeys ranging from a few metres to thousands of kilometres, over land, through air or water (Dingle 2014). Recent advances in tracking technologies for vertebrates (Rutz & Hays 2009) have facilitated the acquisition of high-resolution trajectories of large fish, sea turtles, birds and mammals, and brought about new discoveries related to migration routes, navigational mechanisms, energetic costs and mortality rates during migration (Wikelski *et al*. 2003; Cochran *et al*. 2004; Hays *et al*. 2014; Klaassen *et al*. 2014). Insects are the most speciose, abundant and economically-important group of terrestrial migrants, but in contrast to vertebrates, most species are too small for individual tracking. Knowledge of insect migration thus lags behind that of vertebrates, but nevertheless insects are an interesting group to study, because they are amenable to experimental manipulation and large-scale population studies in ways that vertebrates are not. Furthermore, insects lie at one end of the continuum of self-powered movement capacity versus strength of the flows within which they move. The problem of being drifted off-course by water or air currents applies to all flying and swimming animals, including those capable of much stronger self-powered movements relative to flow speeds (Chapman *et al*. 2011b). How migrating insects are able to deal with the challenge of unfavourable flows lies at the heart of the group's success in achieving long distance population relocations, and the answers to this question will prove insightful for advances in the field of movement ecology (Nathan *et al*. 2008).

A universally-accepted definition of migration applicable to all animal groups has proved difficult to generate (Dingle 2014), but one popular approach has been to focus on the *consequences* of the movements (spatial population dynamics), which has given rise to the huge field of 'dispersal ecology' (Clobert *et al*. 2009; Stevens *et al*. 2012, 2014). Some dispersal ecologists delineate migration rather narrowly – as round-trip animal movements between regular breeding and non-breeding grounds (Clobert *et al*. 2009). Taking this approach, most long-range insect movements would be classed as 'dispersive' rather than 'migratory', because few insect species complete closed-circuit journeys between discrete but regular breeding and non-breeding ranges. In this review we follow Dingle and colleagues, and use a broader definition based on behavioural traits, whereby migration is characterized by persistent, straightened-out movements that are undistracted by the cues which would arrest other types of movements (Dingle & Drake 2007; Dingle 2014). Focussing on the behavioural mechanisms underlying the movement pathways, rather than solely on the ecological outcomes of the movements (the population consequences), is a key strength of this approach (Nathan *et al*. 2008), because natural selection acts on the behaviour/physiology of individuals rather than populations. Use of this broader definition allows a wider variety of long-range insect movements to be classified as migratory, thus enabling commonalties in the evolution and orchestration of migration to be identified across a wide taxonomic spectrum.

In this review, we restrict discussion of migration to large insects (>40 mg) in the Odonata, Orthoptera and Lepidoptera that undertake seasonal movements, involving journeys of hundreds of kilometres. The migrations have some degree of return, and thus these species would be recognised as 'migratory' under both behavioural and ecological definitions of migration. Insect migrations may take place close to the ground within the 'flight boundary layer' (FBL), the lowermost layer of the atmosphere within which the insects' self-powered flight speed exceeds the wind speed, allowing control of migration direction (Srygley & Dudley 2008; Table 1). More commonly, however, migrations take place at high altitude (often hundreds of metres above ground), where migration directions are largely determined by the wind. Migratory movements in the species discussed typically take the form of either: (i) regular northwards and southwards movements within the temperate zone, allowing migrants to track the seasonal advance and retreat of plant productivity in response to temperature changes; or (ii) less predictable movements in response to variable rainfall patterns in arid/semi-arid sub-tropical and tropical zones (Drake & Reynolds 2012). As most insects are relatively short-lived as adults, an individual will normally complete only part of each circuit (i.e. migratory circuits are multi-generational).

The ultimate function of these movements is to allow the rapid exploitation of alternative habitat regions in response to seasonal environmental changes. C*limatic* differences between regions (temperature and rainfall conditions suitable for development) are often assumed to be the fundamental selection pressures favouring migration, but other evolutionary drivers are likely to be important too (as we discuss below). The vagaries of migration-influencing winds, and spatio-temporal unpredictability of habitats, mean that insect migrations have a semi-nomadic element to them, and multiple generations may elapse before descendants return to particular vicinities. Nonetheless, recent studies of the behaviour of migrant insects, *while these movements are in progress*, have led to a significant shift in our perception of the abilities of insects to control their migrations – they are less ‘at the mercy of the wind’ than was previously assumed. We then consider advances in the elucidation of the annual migration routes of long-range insect migrants, which largely remain poorly characterised. These developments have practical implications because the insect migrants include charismatic species of butterflies and dragonflies (May 2013), some of which, e.g. *Danaus plexippus* (monarch butterfly), are of increasing conservation concern (Brower *et al*. 2012); conversely, other species (locusts, various noctuid moths) are important agricultural pests.

We also highlight advances in our understanding of the evolutionary drivers, ecological strategies, and consequences for the population dynamics of these migrants. We discuss newly-documented examples of the benefits of ‘continuous’ movement, including: increased reproductive potential and survival; and lower rates of predation, parasitism and pathogen infection (the ‘enemy release hypothesis’; Coalutti *et al*. 2004). Despite these potential benefits, long-range insect migration will always represent a gamble with large potential rewards or penalties (e.g. Ward *et al*. 1998), and so we discuss recent contributions exploring the trade-offs associated with migration, and mechanisms that insects have evolved to reduce detrimental impacts. Finally, we draw attention to comparisons of migration in insects and vertebrates, and suggest experimental and modelling approaches that may address significant knowledge gaps. Such comparative approaches allow the identification of suites of common traits that are associated with increased movement capacity, and which have been identified in a wide range of species across the animal kingdom, and termed ‘migration syndromes’ (Dingle & Drake 2007) or ‘dispersal syndromes’ (Clobert *et al*. 2009; Stevens *et al*. 2012, 2014).

MECHANISMS FOR CONTROLLING MIGRATORY DIRECTION

Decision rules for initiating migration

In common with many birds, mammals and fish, seasonal migrations of large insects occur on an enormous scale, frequently involving millions of individuals moving simultaneously in the same direction, typically over a large spatial extent (Holland *et al*. 2006; May 2013; Stefanescu *et al*. 2013). The majority of such species do not migrate collectively, but even so mass departures on the same day (or night) must be synchronized in some way. Animal migrants are characterised by specialised pre-departure physiologies, often coordinated by juvenile hormone titres in insects, which in conjunction with environmental cues such as photoperiod, regulate the interaction between migration and sexual maturation. These physiological mechanisms have been extensively studied in, for example, the noctuid moth *Mythimna unipuncta* (McNeil 2011), but this topic falls outside the remit of the current review, where we focus on ecological and behavioural factors orchestrating migration. In obligate migrants (in which all individuals migrate), the cues that stimulate take-off in physiologically-primed individuals are particular light-intensity thresholds and meteorological factors (air temperature, wind speed and atmospheric pressure; Drake & Reynolds 2012). Flight boundary layer (FBL) migrants (see Table 1) are not bound by the prevailing wind direction and can thus take-off and maintain movement in their preferred direction whenever environmental conditions allow, typically when ambient temperatures exceed their flight threshold.

Species migrating above their FBL will, by definition, have their movement direction strongly influenced by the wind, and one might expect departures to be restricted to occasions when high-altitude winds facilitate movement in seasonally-appropriate directions. In some cases relatively simple decision rules seem to be employed to maximise the probability of favourable transport. For example, falling temperatures during autumn promote the initiation of migratory flights in *Vanessa atalanta* (red admiral butterfly; Mikkola 2003) and *Anax junius* (green darner dragonfly; Wikelski *et al*. 2006), thus increasing the probability of windborne transport on cool northerlies towards lower-latitude winter-breeding regions. In other situations, the suitability of high-altitude tailwinds cannot be assessed from simple meteorological cues such as temperature, humidity or atmospheric pressure, and migrants must somehow directly assess the direction of downwind transport during or immediately after take-off. This scenario is exemplified by *Autographa gamma* (silver Y moth), in which mass-migration events are restricted to nights with seasonally-favourable high-altitude winds; *A. gamma* seemingly uses an internal compass sense to assess the direction of its windborne displacement during ascent, and terminates migration if the direction is unfavourable (Chapman *et al*. 2008a, b). Whatever decision rules insects employ to maximise the probability of migrating on favourable tailwinds, behaviours *in-transit* (such as selection of favourable headings and flight altitudes) are still hugely important. We now discuss these behaviours for (i) daytime migrants flying within their FBL, and (ii) day- and (iii) night-time migrants which ascend above their FBL.

Flight behaviour in daytime FBL migrants: cues and mechanisms

The long-distance migrations of day-flying insects such as butterflies and dragonflies are typically thought to take place within the flight boundary layer (FBL). Migrating near the ground in winds that are slower than self-powered airspeeds allows migrants to move in their preferred direction, even in headwinds (Srygley & Dudley 2008; Chapman *et al*. 2011b). There are numerous observations in the literature of day-flying butterflies and dragonflies engaging in mass migration in a seasonally-advantageous direction close to the ground (Srygley & Dudley 2008; May 2013; Stefanescu *et al*. 2013). Maintaining a consistent flight heading requires the use of a compass mechanism; the sun's position in the sky is the principal cue used by daytime migrants, including the monarch (Mouritsen & Frost 2002; Froy *et al*. 2003), the neotropical pierid butterflies *Aphrissa statira* and *Phoebis argante* (Srygley & Dudley 2008), and the painted lady butterfly *Vanessa cardui* (Nesbit *et al*. 2009). In this way, insects parallel a wide range of other day-migrating taxa that rely on a sun compass to maintain a constant heading, including crustaceans, fish, amphibians, reptiles, birds and mammals (Milner-Gulland *et al.* 2011; Dingle 2014; Hansson & Åkesson 2014).

The control of migratory direction has been most intensively studied in the eastern North American population of the monarch butterfly. By late-August, monarchs in north-eastern USA and south-eastern Canada enter reproductive diapause and begin their southward autumn migration to overwintering sites in the mountains of central Mexico, a distance of >3000 km. Autumn migrants use a time-compensated solar compass to fly towards the southwest (Mouritsen & Frost 2002; Froy *et al*. 2003) – the constant compass course towards their overwintering site. In early spring, the overwintered monarchs migrate northwards out of Mexico to recolonize Texas. Spring re-migrants show a seasonal reversal of their migration direction, and now use their solar compass to fly towards the northeast. A period of cold exposure typical of conditions at the overwintering site is, however, necessary to switch the migration direction; if monarchs are kept at constant autumn conditions throughout the winter, they continue to orientate towards the south the following spring (Guerra & Reppert 2013).

Recently there have been considerable advances in understanding the molecular and neuronal mechanisms underlying sun compass orientation in monarch butterflies. To maintain a constant bearing (northeast in spring, southwest in autumn), monarchs must compensate for the azimuthal movement of the sun across the sky, and this requires a circadian clock to provide a timing mechanism (Froy *et al*. 2003). Important elements of this photic-entrainable clock are located in the antennae (Merlin *et al*. 2009; Guerra *et al*. 2012, 2014; Guerra & Reppert 2013). In addition to the well-documented solar compass, there is new evidence that monarchs may also use a back-up magnetic inclination compass when the sun is not visible (Guerra *et al*. 2014). Migratory birds and bats are known to use multiple compass mechanisms in a hierarchical manner, often using a magnetic compass when celestial cues are not available, but using celestial cues to recalibrate their magnetic compass on a daily basis (Cochran *et al*. 2004; Muheim *et al*. 2006; Holland *et al*. 2010). If monarchs do indeed prove to have two (solar and magnetic) compass mechanisms, the nature of the interactions between them will need to be elucidated. Be that as it may, the latest indications are that monarchs reach their Mexican wintering areas by means of a straightforward vector-navigation strategy, i.e. they are not able to determine their geographic position along the route using an internal 'map' (Mouritsen *et al*. 2013; but see Oberhauser *et al*. 2013). Large-scale topographic features probably also help to funnel the migrants towards the overwintering sites, and at closer range the locations of the winter refuges (oyamel fir groves) may be pinpointed by olfactory cues – all these aspects require further study however.

Even FBL migrants will experience lateral displacement by crosswinds ('drift'), and to maintain preferred (seasonally-beneficial) movement directions they must compensate for this effect (Chapman *et al*. 2011b). The varying abilities of neotropical day-flying butterfly and dragonfly migrants to deal with drift have been studied by Srygley and Dudley (2008) in

Panama. The various species show considerable variation in their ability to perceive and compensate for crosswind drift (from ‘complete compensation’ to ‘full drift’). Where compensation occurs, an optomotor response to the apparent motion of the ground is presumably the primary mechanism, although other means of compensation may be involved when butterflies travel over water bodies (such as the use of two landmarks on the shore that are held in parallax). Rather surprisingly, perhaps, some butterflies can still compensate partially for wind drift when flying over the sea, out of sight of land, and without terrestrial cues other than the sea surface itself (Srygley & Dudley, 2008). In addition, one of the butterflies showed tailwind compensation too: female (but not male) *Phoebis sennae* adjust their airspeed according to the degree of tailwind assistance (i.e. they slow their airspeed in tailwinds and increase it in headwinds), an adaptation that optimizes energy consumption during flight, thus conserving lipids for egg production (Srygley & Dudley, 2008). The mechanisms that temperate zone migrant butterflies (e.g. monarchs and painted ladies) use to deal with winds from a variety of directions remain to be elucidated.

Day-flying migration above the FBL

As discussed in the previous section, butterfly migration has typically been assumed to occur exclusively within the FBL, apart from the monarch and Camberwell beauty (*Nymphalis antiopa*) where soaring and gliding behaviour is well documented (see Table 1). Recently, however, evidence has accumulated that butterfly migrations can occur at altitude (up to 1 km above ground) under certain circumstances – presumably the crucial factor being that high-altitude winds are blowing in seasonally beneficial directions (Mikkola 2003; Stefanescu *et al*. 2007, 2013; Chapman *et al*. 2010). For example, Stefanescu *et al*. (2007) found a strong association between spring arrivals of *V. cardui* into northeastern Spain and high-altitude winds from probable source areas in North Africa. Flying at altitude has also been proposed as the reason for the long-standing difficulty in detecting the return migration of *V.*

cardui from northern Europe in autumn (Stefanescu *et al*. 2013). Trajectory analysis of *V. cardui* movements indicates that migration may be continued into the night (Stefanescu *et al*. 2007); this definitely occurred during high-altitude migrations of *Pantala flavescens* (wandering glider dragonfly) over the Bohai Sea in China (Feng *et al*. 2006) and would also apply to the very long migrations postulated for this species over the Indian Ocean (Anderson 2009; Fig. 1). It is well known that cues causing the normal termination of *nocturnal* migrations are over-ridden if the migrants find themselves over the sea at dawn (Drake & Reynolds 2012), and something equivalent presumably occurs at nightfall in day-active taxa. Many questions remain regarding the high-altitude daytime migrations – in particular, we need better documentation of the circumstances in which migrants ascend to altitude, and the mechanisms underlying flight-height selection.

Flight behaviour during high-altitude nocturnal migration

Behavioural traits such as flight orientation, tailwind selection and flight-altitude selection in large insect migrants would seem, self-evidently, to be important elements in optimizing rapid movement in favourable directions, and thus to have major impacts on migration success. Systematic observation of the flight behaviour of insects when they are high in the air, well above their FBL, is highly problematic though. Nonetheless there have been significant advances in our knowledge due to the use of specialized vertical-beam entomological radars (Chapman *et al*. 2011a) (Table S1). The bare fact that high-flying nocturnally-migrating insects often show a degree of common alignment has been known for decades, since radar was first deployed for entomological purposes, but there has been uncertainty over the extent to which the observed orientations are *ecologically* adaptive, i.e. whether effects on flight trajectories would materially enhance migration success (Reynolds *et al*. 2010).

Until recently, the extent to which the progeny of windborne insect migrants reaching high latitude summer-breeding grounds actually achieve mass return migrations to their winter-breeding regions was unknown. This led to suggestions that these seasonal journeys represent a population sink from which there is no return, an idea that was dubbed the “Pied Piper” effect (Stinner *et al*. 1983). While this hypothesis made little evolutionary sense, it held sway because of an apparent lack of return migrations in many species. The advent of specialised entomological radars however has recently demonstrated the existence of mass return migrations in a number of species that invade the North Temperate Zone from further south, effectively refuting this notion (Chapman *et al*. 2012). Some cases elsewhere remain unclear: biogeographical studies of *Spodoptera exempta* (African armyworm) provide little evidence that the offspring of moths which reach the extremes of the migratory range (Yemen and South Africa) ever return to the putative core areas in Kenya and Tanzania (Rose *et al*. 2000; Fig. 2).

The radar-based behavioural studies have particularly concerned the noctuid moth *A. gamma*, which invades northern Europe in variable numbers each year in late spring and early summer from winter breeding areas around the Mediterranean Basin. The spring immigrants (first generation) arrive in northern temperate areas on spells of warm southerly winds and breed immediately; their progeny (second generation) typically emerge in late-summer/early-autumn. The migration of the autumn generation is interesting, because they must move south (and somehow avoid being taken further northward) if they are not to be killed off by frosts, as this species cannot enter diapause. The suite of behaviours that result in beneficial migration directions include: (a) initiation of migration only on nights with seasonally-favourable high-altitude tailwinds; (b) flying at the altitude of the fastest winds (typically 400 – 800 m above ground); (c) adopting a flight heading that partially counteracts crosswind drift from the preferred migration direction; and (d) seasonal reversal of the preferred direction between spring and autumn (Chapman *et al*. 2008a,b, 2010). Migrating *A. gamma* typically achieve ground speeds between 30–100 km per hour, completely overlapping with the speeds of migrating passerines (Alerstam *et al*. 2011). When the wind blows more than 20° away from their preferred direction of travel, the migrants also adjust their headings so that they partially correct for wind-induced drift (Chapman *et al*. 2010). Complete compensation is not observed, and the moths' orientation strategy ('compass-biased downstream orientation'; Chapman *et al*. 2011b) is a trade-off between moving rapidly and in a preferred direction. The reversal of the preferred direction between the spring and autumn generations appears to be controlled by seasonal (probably photoperiodic) cues; in the absence of the correct cues, these consistent migration patterns break down. For example, in a year when the second generation of *A. gamma* emerged unusually early in the UK (July rather than August/September), moth flight behaviour was observed to be highly atypical. Movements were significantly more 'dispersive' and randomly-oriented, occurring on tailwinds from all directions (Chapman *et al*. 2013). In normal years, the observed flight behaviours make a considerable difference to the migration trajectories, as shown by atmospheric dispersion model simulations of passively-transported inert particles compared with particles with *A. gamma*-like flight behaviour. Simulated moths travel significantly further (an extra 100 km per night) and drift a smaller amount (~20°) from the seasonally optimal direction than the passively-advected particles (Chapman *et al*. 2010). Further simulations indicate that most autumn-generation *A. gamma* emigrating south from northern Europe would reach Mediterranean areas suitable for winter breeding within 3 nights of migration (Chapman *et al*. 2012).

CHARACTERIZING MIGRATION ROUTES AND POPULATION TRAJECTORIES

One major objective of determining parts of the flight-paths of insect migrants is, ultimately, to reveal the full *population trajectory* through space and time (Dingle & Drake 2007), but progress with non-locust long-range migrants (e.g. Lepidoptera and Odonata) has been slow. The culmination of research on the monarch butterfly has recently allowed the mapping of migration and colonisation patterns across eastern North America over the annual cycle of five generations (Miller *et al*. 2012; Flockhart *et al*. 2013). Among other techniques, these studies modelled ‘citizen science’ distribution data, examined wing wear to estimate age, and used stable-isotope analysis of wing chitin to estimate natal origin (Table S1). Establishing the importance of the various breeding areas along the monarch’s migration circuit will assist the development of conservation strategies; for example, the importance of the ‘corn belt’ in the US Midwest for monarch breeding has highlighted the issue of the loss of milkweed plants due to new agricultural practices in this region (Pleasants & Oberhauser 2012). Another area of progress is the delineation of the multi-generational migration circuit of the painted lady in the Western Palaearctic (Stefanescu *et al*. 2013) by the collation of numerous citizen-science reports with data from insect-detecting radars. The strategy was shown to be one of continuous breeding with six generations per year, with lengthy movements between each generation, so that the migration circuit may encompass an annual round-trip of 15,000 km between North African and northern European breeding grounds.

Butterflies are unusual in that much of the migration occurs as obvious high-density flights close to the ground and during daylight hours, and so they are particularly well-suited to citizen science observations of migration in action. However, the majority of insects migrate at high altitude (up to 2 km above ground) and often at night, and consequently their migration routes and population trajectories have to be inferred by indirect means, such as trap catches at ground level, population genetics (Fig. 3), radar observations and movement trajectory simulations (Table S1). Population trajectories of most insect migrants are thus incomplete – overwintering areas are usually ill-defined, and the locations where *the bulk* of the population is to be found during winters (or dry seasons) of varying severity is still unclear for most species. In the most extreme example, it has been postulated that the world’s longest insect migration comprises a multi-generational annual migration of *Pantala flavescens* dragonflies from India to East Africa and back again (Anderson 2009; Hobson *et* *al*. 2012; Fig 1); but the return movement, particularly, needs confirmation. Moreover, apart from a few well-studied species such as the monarch butterfly (Brower *et al*. 2012) and *A. gamma* (Chapman *et al*. 2012), the precise contribution of long-range 'return' migrants to winter or dry-season populations under a range of representative conditions is virtually unknown. Thus much work is required to document migration pathways, and until this is done, the migration biology of insects will continue to lag behind that of birds and turtles, where bio-logging studies have resulted in the detailed characterisation of migration routes for numerous species (Rutz and Hays 2009).

EVOLUTIONARY DRIVERS AND ECOLOGICAL CONSEQUENCES

Increased levels of mobility in animals ('migration' or 'dispersal') are typically assumed to impose costs, in terms of lower survival and/or reduced lifetime reproductive success, which may be imposed via several mechanisms. Investment of resources into the development of flight machinery, storage of fuel reserves, and energy expenditure during flapping flight may result in compromised immune systems, and/or reduced fecundity, in birds and insects (Milner-Gulland *et al*. 2011; Bonte *et al*. 2012; Hansson & Åkesson 2014). Additionally, the act of migration itself can be risky – migrating individuals may experience higher mortality rates than non-migrants, due to transport to unsuitable habitats or greater exposure to predators during flight. However, most research on the costs associated with flight activity in insects has focused on relatively short-range dispersive movements, typically in species with wing-length or other flight polymorphisms (Bonte *et al*. 2012). The costs of long-range migration are well known in birds and sea turtles (Sillett & Holmes 2002; Milner-Gulland *et al*. 2011; Hays & Scott 2013; Klaassen *et al*. 2014), but in comparison have been little studied in long-range insect migrants. Apart from increased risk of mortality, migrations encompassing hundreds of kilometres are clearly energetically costly. Equally, migrant species will have evolved mechanisms to offset these costs, but these urgently require further quantification in insects, and this is a research area ripe for exploitation. More progress has been made in quantifying the benefits associated with long-range seasonal migration, and we discuss this next.

Exploitation of seasonal breeding resources

The primary driver of the evolution of long-range insect migration is typically assumed to be escape from environmental conditions incompatible with development. The great majority of insects survive through unfavourable periods in some form of diapause or quiescence. There must therefore be additional benefits that can accrue to migrants beyond escaping deteriorating conditions. Most migrant species breed continuously year-round; consequently, they are capable of more generations per year than phylogenetically-similar non-migrants, and by continuously moving they can potentially exploit a succession of favourable breeding grounds. As long as migrants do not suffer substantially elevated mortality in each generation, or have significantly lower fecundity, migrant lineages thus have the potential for considerably greater reproductive productivity over the course of a year compared with non-migrants.

Supporting evidence for this comes from a recent study of the reproductive benefits of migration in *A. gamma* (Chapman *et al*. 2012). Population monitoring in the UK indicates that summer breeding by spring immigrants results in a four-fold increase in the subsequent generation of adults. This generation embarks upon a southward return to lower latitudes, and simulated migration trajectories suggest that ~80% of immigrants successfully reach destinations where production of the next generation is possible; mortality related to migration is seemingly relatively low, and the reproductive benefits of seasonal migration are transferred to the next generation (Chapman *et al*. 2012). In addition, *A. gamma* has higher fecundity and population growth rates than similar sized non-migrant noctuids (Spitzer *et al*. 1984). Migrant insects invest more in reproductive output than non-migrants, presumably to counterbalance mortality associated with migration, similar to migrant birds (Sibly *et al*. 2012) and a wide range of dispersive taxa including spiders, birds and mammals (Stevens *et al*. 2014). The population data for *A. gamma* therefore indicates that poleward insect migration to exploit temporary breeding resources may confer substantial reproductive benefits, as long as mortality costs associated with migration are not too high. Only a relatively small minority of insects (compared with birds) have evolved long-range migration strategies (e.g. only 3% of the ~500 species of noctuid moths in northern Europe are regular long-range migrants, compared with 44% of songbirds; Alerstam *et al*. 2011) and thus the potential reproductive benefits associated with migration in insects are presumably difficult to realise compared with some other groups.

Movement into enemy-free space

Migration is often assumed to confer additional benefits through successive colonisation of new habitats which temporarily provide an ‘enemy-free space’, or at least a significant reduction in predation, parasitism and/or pathogen infection, compared with remaining permanently in the same location (Altizer *et al*. 2011). For example, Folstad *et al*. (1991) have argued that post-calving migration in Norwegian reindeer is driven by the threat of parasitism by the warble fly *Hypoderma tarandi*; a consequence of which is that the intensity of infection by fly larvae declines with increasing distance migrated. In the case of predation and parasitism rates, the evidence in the entomological literature to support this hypothesis is largely anecdotal, as it is difficult to carry out detailed ‘life-table’ population studies on highly-mobile species. Nonetheless, the older literature on desert locusts clearly suggests that natural enemies have limited effects on gregarious populations, partly because of their general inability to follow the migrating swarms, and partly because the sheer magnitude of large swarms and hopper bands usually exceeds the killing capacity of local predators (Uvarov 1977). Much the same applies to the gregarious caterpillars of *Spodoptera exempta*, an important migratory pest in sub-Saharan Africa. Due to moth migration in each generation, there is little opportunity for parasitoids to build up and kill a significant proportion of the population before it has completed its life-cycle and moved on. If, however, migrants land back in the original breeding area, due to a chance effect of the wind, high levels of parasitism can occur in subsequent larval outbreaks (Rose *et al*. 2000).

A similar increase in the seasonal incidence of parasitism is observed in painted lady butterflies. Data from a large emergence site in the Souss Valley of Morocco revealed that ~10% of caterpillars were killed by the braconid wasp parasitoid *Cotesia vanessae*; but given that each parasitized caterpillar produced an average of 40 wasps, parasitism rates in the next generation of butterflies would be catastrophic *if* they had remained to breed in the same place (Stefanescu *et al*. 2011). Seasonal comparisons of populations within the winter-breeding range (Morocco) and summer-breeding range (north-east Spain) demonstrated that parasitoid populations built up when successive generations of butterflies bred in the same general area: parasitism rates increased from 13% to 66% (Morocco) and from 18% to 77% (Spain) between the first generation colonising the area and the last generation departing (Stefanescu *et al*. 2012). Thus mortality from parasitoids clearly plays an important role in driving the evolution of migration.

Migrants may not completely escape their specialized parasitoids however, as long-range migration can also evolve amongst parasitoids too: for example, *Scelio fulgidus* (a hymenopteran egg parasitoid of the Australian plague locust *Chortoicetes terminifera*) uses the same high-altitude airstreams for windborne displacement as its host (Farrow 1981). The unpredictable nature of windborne movements may benefit potential hosts by reducing the chance of encountering specialised migratory parasitoids, and this may explain why the strategy of migration to communal diapause sites (as found in the monarch butterfly) is comparatively rare. *Agrotis infusa* (bogong moth) also employs this strategy, migrating to mass aestivation sites in the Australian Alps of Victoria to survive the hot and dry summer. During the six months they remain in their aestivation caves, bogong moths experience significant mortality from a parasitic nematode that has become adapted to this regular food source (Common 1954).

Rates of predation experienced by colonising immigrants compared with resident species have not been quantified as far as we know, and so this remains at best a plausible but untested hypothesis. However, there is good evidence that migration to high latitudes significantly reduces predation rates in migratory shorebirds (McKinnon *et al*. 2010), and so it is a topic ripe for exploration in insect systems. Migrants may experience a *greater* risk of predation during the migratory flight itself, which will counteract any benefits of reduced predation rates post-arrival. The spatial distribution of vertebrate aerial insectivores may even be shaped by the availability of large concentrations of migrating insects. For example, >100 million *Tadarida braziliensis* (Brazilian free-tailed bats) migrate from Mexico to Texas each spring, where they form huge colonies and feed on migrating noctuid moth pests at high altitudes (McCracken *et al*. 2008), providing an economically important pest suppression service (Boyles *et al*. 2011). In the case of aerial insectivorous birds such as *Falco amurensis* (Amur falcon), which migrate from southern India to East Africa across the Indian Ocean, it is thought that concurrently migrating *P. flavescens* dragonflies provide in-flight fuelling, and that the dragonfly migration route may have actually shaped the route taken by these birds (Anderson 2009; Fig. 1). Thus, large-scale insect migrations may provide an important driver for the mass aggregations and migration routes of organisms at higher tropic levels.

Migrants may escape predators and parasites when they move into new habitats, but they may also be a source of parasites that could infect local resident populations (Bauer & Hoye 2014). Few examples of this have been documented, but there are a number of instances where invasive species have outcompeted residents by bringing with them infectious disease agents that they themselves are better able to tolerate; a form of ‘apparent competition’ (Strauss *et al*. 2012). A recent possible example is the introduction into Europe of *Harmonia axyridis* (Asian harlequin ladybird). This species hosts a *Nosema*-

like microsporidian that is tolerated by *H. axyridis* due to its production of an antimicrobial alkaloid called harmonine; however, the pathogen is lethal to native European *Coccinella* ladybirds when injected (Vilcinskas *et al*. 2013a). Whether or not microsporidia-induced mortality is a cause of decline in several native ladybirds remains to be confirmed, however, since infection via the gut during intra-guild predation in the field has yet to be established, and other mechanisms for the declines are possible (Vilcinskas *et al*. 2013b). Nonetheless, the potential for migrating insects to carry pathogens into new areas is a very real possibility, especially with current climate-change influences on insect species' distributions (Bebbe *et al*. 2013).

Microbial pathogens and migration

The multifarious effects that microbial pathogens have on animal migration have only begun to be elucidated within the last decade or so, and much remains to be discovered. Movement of infected hosts will of course influence the geographical spread of pathogenic organisms, while on the other hand the physiological and behavioural impacts of (sub-lethal) infections may have important ramifications for migratory performance and population dynamics (Altizer *et al*. 2011; Hall *et al*. 2014). This may lead to complex relationships between pathogens and migration (Box 1, Fig. 2, Fig. 4), and for insects the best studied system is, once again, the North American populations of the monarch butterfly. Monarchs are highly susceptible to infection from a debilitating protozoan, *Ophryocystis elektroscirrha*, which can be lethal to individuals carrying high pathogen burdens. The prevalence of heavily-infected adults is highest in the resident population of monarchs found in Florida, intermediate in the short-range migratory population in the west, and lowest in the long-range migratory population in the east (Altizer *et al*. 2000). The differences in pathogen prevalence between these populations with different migratory tendencies are thought to arise from two non-exclusive mechanisms, and the resulting fitness benefit of lower pathogen prevalence is likely to be a significant driver for the evolution of migration (Altizer *et al*. 2011). In the first mechanism ("migratory escape"), migration allows individuals to escape from environments where pathogens have or will accumulate. Within the eastern population, pathogen prevalence was lowest at the start of the breeding season and peaked at the end of the breeding season, indicating that infection rates do increase with longer residency times (Bartel *et al*. 2011), consistent with the migratory escape hypothesis.

In the second mechanism ("migratory culling"), the physical act of migration reduces the incidence of pathogens in the population because heavily-infected individuals are unable to complete long migrations, due to the combined physiological demands of fighting infection and undertaking a challenging journey (Altizer *et al*. 2011). Eastern monarchs provide evidence for this hypothesis, as heavily-infected butterflies have lower flight performance than healthy individuals (Bradley and Altizer 2005), and pathogen prevalence tends to be lower in individuals that reach the Mexican over-wintering grounds than the average pathogen load in butterflies commencing autumn migration (Bartel *et al*. 2011). In addition, *O. elektroscirrha* isolates from the less migratory Western population of monarchs are more virulent than strains from the eastern population, consistent with the notion that the most virulent strains are removed by migratory culling during the longest migratory flights (de Roode and Altizer 2010). This body of work provides a compelling argument that migration delivers significant fitness benefits by reducing pathogen infection rates, and thus it is likely that avoidance of infectious diseases has been a significant driver of the evolution of long-range migration in monarchs, and probably other migrant species (Hall *et al*. 2014).

In contrast, levels of the endemic baculovirus, *Spodoptera exempta* nucleopolyhedrovirus (SpexNPV), accumulate during the migratory outbreak season of the African armyworm (Fig. 2), in part due to the propensity for the virus to be *vertically*-transmitted from parents to offspring, so allowing the pathogen to 'migrate' along with its host (Vilaplana *et al*. 2010; Graham *et al*. 2012). Whilst this might at first appear to be at odds with the enemy-release hypothesis, it is clear that failure to migrate at each generation would result in mass mortality due to enhanced *horizontal*-transmission of virus at the natal breeding site. Indeed, even with migration partially ‘resetting the clock’ of virus population levels at each generation, larval mortality may still reach 98% in late-season larval outbreaks (Rose et al. 2000), suggesting that avoidance of baculovirus infections is a significant selection pressure favouring migration. More studies of this kind are required to establish how widespread this evolutionary process is in other insect migrants.

There is also a pressing need to establish the exact nature of the interactions between migration and pathogens, and how these vary across host and pathogen species and genotypes. For example, we know little about the shapes of the norms of reaction between pathogen load and migratory capacity, or between migratory effort and susceptibility to infection (Box 1, Fig. 4). Given that migratory flight and immune function are both known to be physiologically costly (Rankin & Burchsted 1992; Schmid-Hempel 2011), it seems inevitable that these two processes are intimately linked. Quantifying the shapes of these cost functions (Fig. 4), via laboratory infection trials and tethered flight mills (Fig. 5; Table S1), for example, will allow us to make more specific predictions about the likely evolutionary trajectories of these two traits.

An additional mechanism by which individuals can reduce their risk of infection from pathogenic microbes during population build-ups is to invest more resources into their immune system. In the case of migratory insects, this is particularly evident in those species that invest relatively more in pathogen resistance mechanisms when occurring in high-density populations (where horizontal transmission rates will be higher) – a phenomenon known as density-dependent prophylaxis (DDP) (Wilson *et al*. 2001). Immune defences are costly, and so complex trade-offs will presumably exist between migratory capacity, pathogen load and immune responses; these trade-offs have proven difficult to quantify however. *Spodoptera exempta* exhibits DDP, investing relatively more in pathogen resistance under the high-density conditions that prevail during outbreaks (Wilson *et al*. 2001), reducing their susceptibility to the SpexNPV baculovirus. It may be predicted therefore that crowded larvae (which invest more in immunity) will have lower migratory performance as adults, but in fact the converse appears to be true (Woodrow *et al*. 1987). This may be because the same (density-related) cues that trigger DDP also stimulate elevated flight and that the costs of both are subsumed elsewhere (Fig. 4a), but the precise relationships between migratory propensity, flight performance, immune responses and pathogen load remain to be quantified. A study of a plant and its fungal pathogen suggests that interactions between dispersal, immunity and disease are likely to be complex (Jousimo *et al*. 2014). Modelling studies suggest that even in the absence of this complexity, the optimal migration strategy is critically dependent on the prevalence of pathogens in the population and that the vulnerability of populations to emerging infections can depend on their current migratory habits. Moreover, factors which affect the distance or timing of migration (land-use change, climate change, etc.) could increase pathogen prevalence; an effect that has already been documented in some vertebrate species subject to anthropogenically-induced migratory shifts, including the emergence of Hendra virus in fruit bats, ectoparasitic sea lice in wild salmon, and brucellosis infection in elk (Hall et al. 2014). It seems likely that similar effects will be seen in insect systems too.

FUTURE PERSPECTIVES

This is an exciting time to be engaged in insect migration research, as many of the questions requiring answers are now tractable due to advances in telemetry (Kissling *et al*. 2013), remote sensing (Drake & Reynolds 2012), stable isotopic analysis (Hobson *et al*. 2012) and genomic (Liedvogel *et al*. 2011) technologies (Table S1). As the genomes of migratory insects, such as the monarch butterfly (Zhan *et al*. 2011) and *Locusta migratoria* (migratory locust) (Wang *et al*. 2014), are published, they will offer new insights into the evolution and organisation of migration. For example, the sequencing of multiple genomes of monarchs from migratory North American populations and non-migratory populations from across the globe have produced fascinating revelations about the evolutionary history of monarch migration and the genes underlying the syndrome (Zhan *et al*. 2014). The results of this comparative sequencing indicate that the ancestral monarch population inhabited temperate North America and was migratory, and that all three sub-tropical/tropical resident populations (Central/South America; Pacific; and Atlantic lineages) were independently derived from migrants originating in North America (Zhan *et al*. 2014). More surprisingly, all three transitions from migratory to non-migratory behaviour were associated with reversion to an ancient (non-migratory) haplotype containing a version of the collagen IV gene that is associated with a reduction in muscle efficiency and flight performance (Zhan *et al*. 2014). These results indicate that migration may evolve and regress frequently and rapidly, and the physical act is reliant on efficient muscle function, but there is still much to learn about the genetic and epigenetic mechanisms which regulate migration (ffrench-Constant 2014; Hansson & Åkesson 2014).

One promising approach for gaining fundamental insights into the ecology and evolution of insect migration is comparative studies of movement patterns in distantly-related taxa, whether they are walking, swimming, floating or flying migrants (Alerstam *et al*. 2011; Chapman *et al*. 2011b; Reynolds *et al*. 2014). Recent meta-analyses of animal migrations demonstrated that maximum distances are predicted by a model incorporating mass-dependent costs of movement for each mode of locomotion, in animals as diverse as dragonflies, sea turtles, wildebeest and blue whales (Hein *et al*. 2011; Hays & Scott 2013). As predicted by the model, maximum migration distance is positively correlated with body size, and thus among flying animals, insects have relatively short *absolute* migration distances. However, when migration distance is scaled to body size, the longest insect migrations (Lepidoptera and Odonata) are approximately 25 times longer than migration distances of the largest birds (Hein *et al*. 2011). One of the reasons that insects can seemingly outperform the largest and strongest flying birds in terms of relative migration distance is the highly efficient strategies they have for acquiring the maximum degree of wind assistance (Alerstam *et al*. 2011). Comparative studies such as these have shown that, contrary to widely-held perceptions that insect migration represents a risky and wasteful process, some insects are in fact amongst the most efficient, successful and longest (scaled to body size) migrators.

One of the least well studied aspects of insect migration is the effect that mass arrivals of immigrants have on the ecosystems they periodically invade (Bauer & Hoye 2014). The consequences of a sudden influx of millions or even billions of migrant insects to temperate zones each spring, followed by the departure of sometimes even greater numbers to lower latitudes each autumn (Chapman *et al*. 2012), have hardly been investigated. These seasonal transfers involve enormous quantities of biomass, nutrients and a multitude of associated pathogenic and endosymbiotic microbes. The effects may be positive (e.g. delivery of ecosystem services such as pollination, biological control of pests and provision of food to higher trophic levels) or negative (e.g. spreading infectious plant and animal diseases and reducing agricultural crop yields), to both resident biodiversity and human society (Bauer & Hoye 2014). Elucidating the diverse impacts of a mass arrival of insect migrants on ecosystem function remains a challenging prospect, but the first stage is to accurately quantify the numbers of insects involved in these movements. To the best of our knowledge, this has been achieved for only one species (*A. gamma*) invading one country (the UK), where invasions of up to 250 million moths can arrive during spring (Chapman *et al*. 2012); more studies of this kind are urgently needed. Quantifying insect migration over large spatial scales remains problematic, but new opportunities to study the long-range movements of comparatively small animals through the aerosphere, using continental-scale networks of radars (Chilson *et al*. 2012; Shamoun-Baranes *et al*. 2014) and the ICARUS initiative for a global small-animal satellite tracking system (Wikelski *et al*. 2007), hold considerable promise that this may become feasible in the near future. Given the effect that anthropogenic climate change and land-use change may have on the migration strategies of economically important pest species (Bebbe *et al*. 2013), such continental-scale monitoring programs will become increasingly important.

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Figure Legends

Figure 1. A schematic indication of the proposed migration route of *Pantala flavescens* (wandering glider dragonfly). The thin light-blue arrow shows the autumn migration from India across the Indian Ocean via the Maldives, Chagos, Seychelles and Aldabra to east Africa. Months indicate arrival dates of large numbers of *P. flavescens* at locations across the Indian Ocean. The broad light-blue arrow indicates the north-easterly winds at altitudes above 1000 m behind the (southward-moving) Inter-tropical Convergence Zone, which the dragonflies use for transport. It is suggested that there is a reciprocal migration to India in May on the winds of the Somali Low-Level Jet (broad dark-blue arrow). Predatory Amur falcons (*Falco amurensis*) and other aerial insectivorous birds follow the same migratory route, and may prey on the dragonflies during the journey. (Modified from Anderson, 2009; photo of *P. flavescens* copyright 2011 dragonflywoman.wordpress.com; photo of *F. amurensis* copyright 2011 M. Putze birdsmongolia.blogspot.co.uk).

Figure 2. Migration and viral disease intensity in *Spodoptera exempta* (African armyworm) in eastern Africa. (a) Known primary outbreak areas and typical movements during a major outbreak season (figure and photo from Rose et al. 2000). Dark shading shows the locations of reported high-density, early-season larval outbreaks; dappled shading is areas where unreported outbreaks are suspected; dotted shading is large water bodies; and solid arrows are the migratory movements of moths initiating new outbreaks. Migration direction is determined by seasonal wind patterns and movement of the Inter-tropical Convergence Zone, and the location of outbreaks is governed by the seasonal patterns of rains, typically occurring in areas of low and erratic rainfall. (b) As the rainy season progresses and the number of larval outbreaks increases, the larval viral loads and the prevalence of virus-induced mortality increases, even though moths migrate at each generation (data from Graham et al. 2012).

Figure 3. An example of long-distance insect migration routes inferred from genetic methods, namely the geographical distribution of *haplotype ratios* in the 'corn strain' of *Spodoptera frugiperda* (fall armyworm moth). The open light blue oval and dark blue circle estimate the extent of the overwintering range in Texas and Florida, respectively. Fall armyworm can also overwinter in the Caribbean but whether these populations contribute to those in Florida is still a matter of speculation. Light blue arrows indicate putative direction of the migration from the Texas–Mexico overwintering areas. Dark blue arrows depict movement from Florida populations. Lined circles show approximate locations of "hybrid zones" where the two migratory pathways appear to overlap. The diagonal green line follows the major elevations of the Appalachian Mountain range, which appears to have a role in segregating the migration pathways. (From Nagoshi *et al*. 2012; photo copyright Wikipedia.org).

Figure 4. The interaction between migration and disease. (a) As pathogen loads increase, we might expect there to be a cost in terms of migratory capacity. This cost may be linear (blue line), non-linear (green), a step-function (red) or negligible (purple), depending on specific circumstances (see Box 1); low-level infections may also act as a cue triggering enhanced migratory capacity (orange). (b) Likewise, as migratory effort increases, so we expect a physiological cost, in terms of enhanced susceptibility to disease, and the shape of this cost function may also take a range of forms, with consequences for the evolution of migration and disease resistance. When costs exceed some threshold, then we can expect migration-induced susceptibility to infection to result in 'migratory culling' (shaded area), *sensu* Altizer et al. (2011); again, the point at which this threshold is reached will depend on the shape of the cost function.

Figure 5. An example of a tethered flight mill for studying migratory flight duration under controlled conditions. (a) Schematic diagram of an individual rotational ('roundabout') flight mill, showing the low-friction magnetic suspension which enables comparatively small and weak-flying insects to engage in sustained flight. Multiple flight mills can be run simultaneously, so that highly-replicated samples of flight data can be collected under identical controlled environmental conditions, enabling study of (for example) the effect of sub-lethal infections on flight capacity. This Rothamsted flight mill design is patent pending (UK Patent Application No. 1314415.9). (b) Experimental moths, such as this *Helicoverpa armigera* (cotton bollworm), have a short 'handle' attached to the dorsal surface of the thorax some hours before nocturnal flight measurement. They can be fed with sucrose solution (lower panel) before being attached to the flight mill arm (upper panel). Figure and photos courtesy of Rothamsted Research Visual Communications Unit.

Box 1. The interaction between migration and disease

There is a two-way interaction between migration and infectious disease, mediated in part by the physiological costs associated with flight and pathogen resistance/tolerance mechanisms. As pathogen loads increase (due to increased exposure and/or lowered resistance), so we might expect the capacity for migration to decline, due to the physiological costs associated with parasitism, possibly resulting in death during migration ("migratory culling", *sensu* Altizer et al. 2011). This cost function may be linear, non-linear, a step function, or negligible (Fig. 4a), depending on the host species, the virulence of the pathogen and/or the type of migration (e.g. flight boundary layer or windborne migration). As an example, in monarch butterflies, flight capacity measured using a tethered flight mill apparatus (Fig. 5), was lower in individuals parasitized by the protozoan *Ophryocystis elektroscirrha* than in uninfected individuals, indicative of a parasitism cost. But, amongst parasitized butterflies, there was no significant relationship between parasite burden (spore load) and either total distance flown or flight speed, suggesting that the relationship may be a step function (Bradley & Altizer 2005). There is a further possibility, which is that low-level exposure to a pathogen could act as a cue triggering an increase in migratory capacity (orange line) as a prophylactic response to avoid further exposure to the pathogen by the individual or their offspring (Wilson et al. 2001). There is a reciprocal relationship between migration and disease: as migratory effort increases (e.g. flight speed/duration, investment in flight muscle mass, etc.), so we might expect susceptibility to the effects of infection to increase and/or for disease tolerance to decline, as resources that might otherwise be directed at combating the infection are re-allocated to fuel migratory flight. When combined and interactive costs of migration and infection exceed some critical threshold, then we can expect there to be 'migratory culling'. Again, the shape of this relationship will vary across host-pathogen systems (Fig. 4b) and so the point at which this threshold is reached will depend on the shape of the cost function. To characterise these migration-induced cost functions requires an experimental approach in which migratory effort and pathogen loads are manipulated, to take account of differences in host condition, immune competence and innate capacity to migrate. We know of no such studies to have yet taken this experimental approach.