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# Mechanisms and Consequences of Partial Migration in Insects

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Partial migration, where a proportion of a population migrates, while other individuals remain resident, is widespread across most migratory lineages. However, the mechanisms driving individual differences in migratory tendency are still relatively poorly understood in most taxa, but may be influenced by morphological, physiological, and behavioral traits, controlled by phenotypic plasticity and the underlying genetic complex. Insects differ from vertebrates in that partial migration is often associated with pronounced morphological differences between migratory and resident phenotypes, such as wing presence or length. In contrast, the mechanisms influencing migratory tendency in wing-monomorphic insects is less clear. Insects are the most abundant and diverse group of terrestrial migrants, with trillions of animals moving across the globe annually, and understanding the drivers and extent of partial migration across populations will have considerable implications for ecosystem services, such as the management of pests and the conservation of threatened or beneficial species. Here, we present an overview of our current but incomplete knowledge of partial migration in insects. We discuss the factors that lead to the maintenance of partial migration within populations, and the conditions that may influence individual decision making, particularly in the context of individual fitness and reproductive tradeoffs. Finally, we highlight current gaps in knowledge and areas of future research that should prove fruitful in understanding the ecological and evolutionary drivers, and consequences of partial migration in insects.

**Keywords: animal migration, flight capacity, intraspecific variation, insect migration, migratory potential, movement ecology, wing polymorphism**

## INTRODUCTION

Vast numbers of animals migrate seasonally across large geographic scales, usually due to shifts in resource availability—indeed, the importance of habitat ephemerality as a primary driver of insect migration has long been recognized (Southwood, 1962; Denno et al., 1991; Dingle, 2014)—and also in response to increased predation, parasitism and pathogen pressure (Altizer et al., 2011; Chapman et al., 2015). Migrants connect habitats and populations through their annual movements, but also have profound effects on ecosystem processes such as nutrient fluxes and the provision of ecosystem services (Bauer and Hoye, 2014; Bauer et al., 2017; Wotton et al., 2019). There is no universally accepted definition of migration, and many authors take a restricted "vertebrate-centric" view and define migration as round-trip movements between discrete "breeding" and "non-breeding" locations, which inevitably excludes most insect examples from this definition. In our review, we adopt a broader view of migration, based on the behavioral definition of Kennedy and Dingle, defined as any movements which are persistent and straightened-out, and characterized by some (temporary) inhibition of behaviors associated with feeding or reproduction (Dingle, 1996, 2014; Dingle and Drake, 2007; Chapman and Drake, 2019). The function of migratory movements is, of course, spatial relocation, but this shift to new habitats is best viewed as a population-level outcome of the individual behaviors. In other words, migration is *defined* as a behavioral process, with the consequences *explained* at the ecological or evolutionary level. Other movement ecology researchers might categorize some of the examples we provide in our review as dispersal instead of migration, but we adopt this broad view in order to discuss insect examples in the context of the established framework for partial migration.

"Partial migration," whereby part of a population remains resident while the rest migrates, is a common phenomenon among migratory species (Lack, 1943; Lundberg, 1988; Dingle, 1996, 2014; Chapman et al., 2011; Kokko, 2011; Shaw and Levin, 2011), and has been reported from a wide range of taxa such as fish (Chapman et al., 2012), birds (Nilsson et al., 2011), and mammals (Mysterud et al., 2011; Berg et al., 2019). However, the term has been little used in studies of insects and other invertebrates (but see Hansson and Hylander, 2009; Attisano et al., 2013; Slager and Malcolm, 2015; Dällenbach et al., 2018; Ruiz Vargas et al., 2018; Vander Zanden et al., 2018). Partial migration arises through intra-population variation in migratory tendency, may be driven by physiological, morphological, or behavioral variation (Chapman et al., 2011), and has been proposed to be an early evolutionary stage in the transition to full migration (Berthold, 2001) but, in insects, it could also mark a reversion to residency. Frequency distributions of insect flight duration are often sharply skewed, with short flights significantly more common than long flights (Davis, 1980). Therefore, if short migratory flights become adaptive because overwintering *in situ* in temperate areas becomes favorable due to warming conditions, short fliers could swiftly replace long-distance migrants in the population. Changes in the frequency of morphs indicates that there must be strong selection for long-distance insect migration to be maintained in the face of the higher mortality rates, physiological costs, and delays to breeding associated with migration (Roff and Fairbairn, 1991; Zera and Denno, 1997; Fox and Dennis, 2010; Bonte et al., 2012; Chapman et al., 2015).

The mechanisms influencing the incidence of partial migration within populations are not well-understood. Three types of partial migration are often recognized in the literature, "breeding," where a population remains together during the non-breeding season, but migrants and residents breed separately, "non-breeding" where a population breeds in the same habitat, but migrants and residents spend the non-breeding season separately and "skipped-breeding" where a population spends the non-breeding season in one location, but part of the population remains and does not breed, while the other migrates to breed (Chapman et al., 2011; Shaw and Levin, 2011; Dingle, 2014). However, these definitions are based on organisms with separate breeding and non-breeding areas, which is often inapplicable to migratory insects, many of which continuously breed year-round with several generations required to complete the migratory cycle (Flockhart et al., 2013; Stefanescu et al., 2013; Chapman et al., 2015). Furthermore, in contrast to vertebrates, migratory insects can show extreme morphological variation between generations, with the production of macropterous morphs, which are long-winged and can undertake migratory flights, brachypterous or micropterous morphs which are short-winged and sedentary, and apterous morphs which are wingless. Short-winged and wingless morphs are unable to migrate and are hereafter referred to collectively as short-winged forms (Johnson, 1969; Roff and Fairbairn, 1991, 2007; Gatehouse and Zhang, 1995; Zera and Denno, 1997; Dingle, 2014). In other cases, the ability to migrate may depend on traits other than wing-length, such as size of the flight muscles or fuel reserves. Thus, whether an individual is migratory or not may come from a "decision" based upon the context in which it finds itself or be pre-determined, for example maternally, as can occur in Hemiptera (Gatehouse, 1994; Vellichirammal et al., 2017).

Here we present an overview of what is known about the incidence and maintenance of partial migration, which is widespread in insects. We contrast the phenomenon in insects and vertebrates, and examine the current terminology used to define the types of partial migration. Knowledge gaps, and fruitful areas for future research, are highlighted. Finally, we argue that insects, with their developmental plasticity and short generation times, provide excellent subjects for investigating the mechanisms that influence migratory decisions.

## PARTIAL MIGRATION IN INSECTS

Insect immature stages (eggs, larvae, nymphs, and pupae) are typically comparatively sedentary compared to adults, so inter-individual differences in migration propensity are generally a feature of the adult stage. Partial migration has been described in a number of insect species from a broad range of orders, such as Hemiptera, Orthoptera, Lepidoptera, Diptera, and Odonata (**Figure 1**), but much of the work on variation in migratory potential has focused on wing-dimorphic hemipterans (Johnson, 1969; Gatehouse and Zhang, 1995; Zera and Denno, 1997; Roff and Fairbairn, 2007; Dingle, 2014). In all cases, it is assumed that an individual will either migrate or remain more-or-less sedentary in one or another life stage in order to increase its overall fitness.

In contrast to most vertebrates, migrant insects are relatively short-lived and usually undergo multiple generations within a year (Chapman et al., 2015). Consequently, defining partial migration into the three main types developed primarily for vertebrates (Chapman et al., 2011; Shaw and Levin, 2011) is inappropriate for insects, particularly due to their short generation times. Some authors have adapted the existing

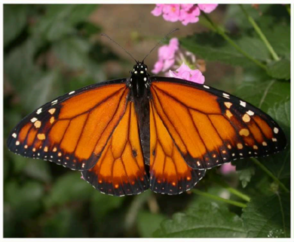
| Species | | | Evidence for partial migration |
|---|---|---|---|
| Wing polymorphic |  | Brown planthopper<br>(*Nilaparvata lugens*)<br>Hemiptera, Delphacidae | Colonisation of new habitat results in an increased proportion of short-winged individuals that have higher fecundity than migrants (Lin et al., 2018). Increased density or decreased resource quality results in a higher proportion of long-winged individuals (Matsumura, 1996). |
| |  | Milkweed bug<br>(*Oncopeltus fasciatus*)<br>Hemiptera, Lygaeidae | Variation in migratory tendency between and within populations (Dingle et al., 1980). Overwintering can occur when the environment is favourable (Dingle, 1982). Resident females show higher rates of oosorption than migrants (Attisano et al., 2013). |
| |  | Sand Cricket<br>*(Gryllus firmus)*<br>Orthoptera, Gryllidae | Long-winged individuals are capable of migratory flight, whereas short-winged morphs are not. Short-winged females have larger ovaries and produce more eggs (Roff and Fairbairn, 2007). |
| Wing monomorphic |  | Southern Monarch<br>(*Danaus erippus*)<br>Lepidoptera, Nymphalidae | Occurs in some areas as mixed populations of migrants and non-migrants (Slager and Malcolm, 2015). Shows elevation and latitudinal migration. Migrants from southern part of the distribution show larger wings and reduced egg production (Slager and Malcolm, 2015). |
| |  | Marmalade hoverfly<br>(*Episyrphus balteatus*)<br>Diptera, Syrphidae | Some may overwinter in the breeding grounds as adults, but also as eggs, larvae or pupae (Raymond et al., 2014). Behavioural differences are present between migratory phenotypes (Odermatt et al., 2017; Dällenbach et al., 2018). |
| |  | Green darner<br>(*Anax junius*)<br>Odonata, Aeshnidae | In northern North America, *A. junius* may overwinter in larval diapause, or migrate south as adults (Corbet, 1999; Freeland et al., 2003). Differences have been seen in developmental time and wing morphology of migrants and residents (Trottier, 1971; Freeland et al., 2003). |

**FIGURE 1 |** Examples of insect species where partial migration has been studied. In all cases presented here, the migratory cycle consists of a number of generations annually and the proportion of migrants and non-migrants may change between generations. Images: *N. lugens*, Y. He; *O. fasciatus*, J. Gallagher (CC BY 2.0); *Gryllus firmus*, D. Roff; *D. erippus*, G. Ruellan (CC BY 3.0); *E. balteatus*, W. Hawkes; *A. junius*, M. Ostrowski (CC BY-SA 2.0).

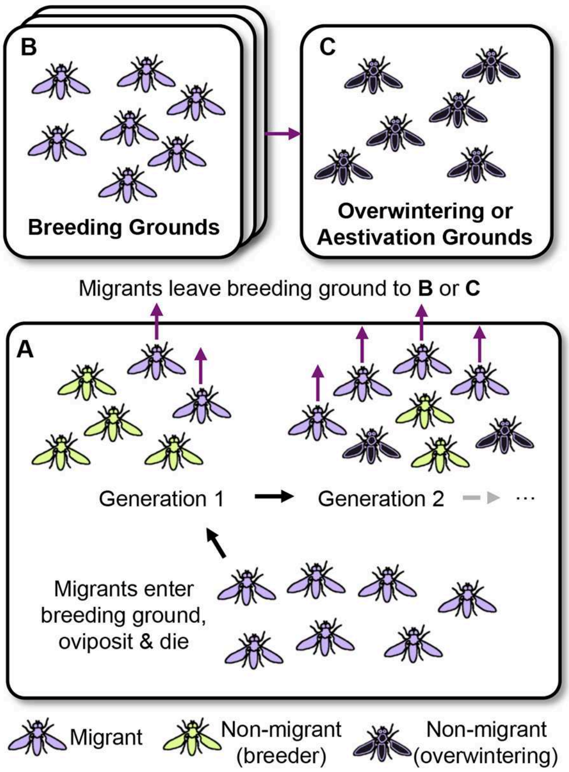


**FIGURE 2 |** Partial migration in insects. **(A)** Migrants (colored purple) enter a breeding ground from a previous breeding, overwintering, or aestivation ground. In a northern temperate system this ground may be at lower latitudes. The migrants oviposit creating generation 1 that consists of a varying degree of migrants (purple) and non-migrants (green) depending on the conditions encountered (photoperiod, temperature, resources, population density). Non-migrants act as resident breeders (for example summer generations of monarch butterflies and migratory hoverflies or various flightless morphs of polymorphic species), producing additional generations in the breeding ground that may also consist of varying amounts of migrants or non-migrants. In contrast, the migrants move away from the breeding area becoming *temporally* separated from the non-migrants, a situation termed *sequential partial migration* (Ruiz Vargas et al., 2018). **(B)** *Migration to breeding grounds* (Class I; Johnson, 1969). Migrants may enter a second breeding ground and the process depicted in **(A)** continues (and may do so over multiple additional areas). Separate breeding grounds may vary through latitudinal or altitudinal and seasonal clines, and the relative fitness of each morph may vary between successive areas depending on conditions. Migration with multiple phases typically consists of relatively short-lived insects, or morphs of a particular species. Continuously breeding species such as the painted lady butterfly may cycle through this system, while other species may only undertake part of it, for example, aphids, planthoppers and spring migrations of hoverflies (see text for other examples). **(C)** In some cases, a species may switch to *migration to overwintering or aestivation grounds* (Class III; Johnson, 1969). Insects with long-distance migration are often relatively long lived, examples include autumn morphs of migrant hoverflies, monarch butterflies and bogong moths. However, overwintering may also take place *within* the breeding grounds without migration (colored black), such as for migratory hoverflies and the green darner dragonfly. Typically, migration or breeding continues again in the spring.

definitions to suit insects, coining terms such as "sequential partial migration," where migratory and non-migratory animals are separated temporally, rather than spatially (Ruiz Vargas et al., 2018), or "alternate migration," to reflect that some migratory individuals switch from a migratory to a non-migratory strategy upon encountering a resident population (Vander Zanden et al., 2018). In many cases, sequential partial migration appears apt, as the proportion of migratory and non-migratory individuals change between generations and this definition reflects the multi-generational aspect of insect migration (**Figure 2**). Broad definitions, such as that a population with 1–99% migrants can be considered as partially migratory (Chapman et al., 2011), will obviously promote the inclusion of insect taxa. A number of hypotheses have been raised to understand the mechanisms driving individual variability in migratory tendency, and these are discussed further below.

## Morphological Variation Between Migrants and Non-migrants

In comparison to vertebrates, insects can show extreme wing polymorphisms between migratory and non-migratory phenotypes. Consequently, partial migration in insects needs to be considered in terms of the contrast between wing-monomorphic and wing-polymorphic species, as there are likely to be different mechanisms and selection pressures acting on these two fundamentally different types. As most work on the trade-offs between migration and residency has been conducted on wing-polymorphic species, comparing migratory and sedentary phenotypes in wing-monomorphic insects may prove useful for elucidating the underlying mechanisms, but such studies are rare (Tigreros and Davidowitz, 2019).

In birds, there are many examples of differences in body size between migrants and residents, with the latter often being larger, possibly due to larger-bodied individuals having a greater physiological tolerance to overwintering (Ketterson and Nolan, 1976; Belthoff and Gauthreaux, 1991) or the ability to endure periods of low resource availability (Boyle, 2008; Jahn et al., 2010; Chapman et al., 2011). In insects, migrants are often larger than non-migrants (Roff and Fairbairn, 2007), a pattern that has been demonstrated for wing-dimorphic species such as the milkweed bug (*Oncopeltus fasciatus*) (Hegmann and Dingle, 1982), and gerrid (water-strider) bugs (Fairbairn, 1992), as well as wing-monomorphic species (Altizer and Davis, 2010). Differences in wing loading and morphology have also been reported between migratory and non-migratory monarch (*Danaus plexippus*) and southern monarch (*D. erippus*) butterflies, with migrants having larger, more pointed wings and higher wing loads than residents (Dockx, 2007; Altizer and Davis, 2010; Slager and Malcolm, 2015; Vander Zanden et al., 2018), which should result in more fuel-efficient flight (Roff and Fairbairn, 1991; Rankin and Burchsted, 1992). Interestingly, no differences in wing morphology were reported between overwintering adults and migrants of the marmalade hoverfly (*Episyrphus balteatus*; Raymond et al., 2014b). There was also no difference in resting metabolic rate between sexes in *E. balteatus*, but the smaller females were shown to have higher evaporative water loss than the larger males (Tomlinson and Menz, 2015).

## Reproduction or Migration?

The costs of migration in relation to reproductive fitness differ between the sexes such that some authors consider that males and females should be considered separately (Johnson, 1969; Gatehouse and Zhang, 1995); here we primarily discuss the relationship as it relates to females. Insect migration is often considered in the context of the "oogenesis-flight syndrome," which posits a trade-off between migration and reproduction (Johnson, 1969; Gatehouse and Zhang, 1995; Dingle, 1996). Development of flight muscles, and migratory flight itself, are energetically costly (Dudley, 1995; Dingle, 2014) and, whereas non-migrants can immediately allocate resources to breeding, migrating individuals will often spend time in reproductive diapause (Johnson, 1969; Rankin and Burchsted, 1992). Migration often occurs pre-reproductively (Gatehouse, 1994; Gatehouse and Zhang, 1995), with reproductive maturity being linked to the cessation of migration, or even the termination of diapause following a period of aestivation or overwintering (Johnson, 1969). However, there is sometimes a more nuanced relationship between reproduction and development of the flight apparatus in wing-monomorphic insects (Rankin et al., 1986; Sappington and Showers, 1992), with some species even migrating with fully-developed oocytes (May et al., 2017; Tigreros and Davidowitz, 2019).

The trade-off between migration and reproduction can be modulated by resource availability in both wing-monomorphic and dimorphic species (Roff and Fairbairn, 2007; Ruiz Vargas et al., 2018). In wing-dimorphic species, the production of macropterous individuals is often determined in early developmental stages or even maternally (Gatehouse, 1994; Wilson, 1995; Ogawa and Miura, 2014; Vellichirammal et al., 2017). Host quality strongly influences wing-morph in brown planthoppers (*Nilaparvata lugens*); upon colonization of a new resource patch, there is an increased proportion of short-winged individuals, which are unable to migrate but have a greater reproductive potential than the macropterous morph (Lin et al., 2018). As the rice crop matures there is an increase in the proportion of the macropterous form, which can migrate to colonize new rice fields, but the proportion of long-winged individuals within a population can vary between seasons and years (Hu et al., 2017). In aphids, the production of winged morphs may be influenced by environmental conditions such as crowding, decreasing food quality, or the presence of predators (Müller et al., 2001). In wing-monomorphic species, or in long-winged individuals of dimorphic species, the ability to respond to changes in resource availability and switch between a migratory and non-migratory state or vice versa may be driven by differences in physiology, such as the ability to reallocate nutrients from flight to reproduction. Indeed, Attisano et al. (2013) demonstrated that resident female milkweed bugs showed a higher level of oosorption (where females resorb nutrients from developing oocytes thus favoring survival over current reproduction) than did migrants.

## Density Dependence

It has been predicted that an increased proportion of migrants should occur in populations at higher densities (Chapman et al., 2011). In insects, partial migration may allow individuals that move to breed to avoid the negative consequences of resource competition (Taylor and Taylor, 1983; Dingle, 1996). For example, in the planthoppers *N. lugens* and *Sogatella furcifera*, an increased proportion of long-winged individuals may be produced at high densities (Matsumura, 1996; Lin et al., 2018). Similarly, crowding can promote the production of winged offspring in aphids (Johnson, 1969; Müller et al., 2001). The lower fecundity typically found in winged forms typically is an example of the tradeoff between the colonization of new habitats and reproductive output.

## Predation and Parasitism Risk

Partial migration may confer some reduction in the risk of predation or parasitism, by movement into an enemy free space, resulting in improved survival for migrants. However, the role of trophic interactions has received relatively little attention in the partial migration literature (Chapman et al., 2011) and has rarely been studied in migratory insects (Altizer et al., 2011; Chapman et al., 2015). Nonetheless, there is evidence that migration can reduce the prevalence of infection from the protozoan parasite, *Ophryocystis elektroscirrha* in monarchs (Bartel et al., 2011; Altizer et al., 2015; Flockhart et al., 2018), with resident populations having higher infection rates than migrant populations (Satterfield et al., 2015, 2016, 2018), providing evidence of "migratory escape" (Altizer et al., 2011) from contaminated environments.

## The Evolution, Expression, and Maintenance of Partial Migration

Migratory flight tendency has been shown to be heritable in a broad range of insect species, indicating a strong genetic component to migratory behavior (Wilson, 1995; Dingle, 1996, 2014; May et al., 2017; Dällenbach et al., 2018). The capacity of insects to form migrants or non-migrants from within the same population could potentially be determined by genetic polymorphisms, for example alleles that influence flight or timing (Niitepõld et al., 2009; Hut et al., 2013; Zhan et al., 2014) and/or the expression of environmentally-induced phenotypic plasticity. While evidence for a solely genetically determined difference is lacking for partial migration, phenotypically plastic pathways are a widespread feature of insect life histories (Nijhout, 1999) and are likely to provide the predominant mechanisms allowing migrants to switch forms, an idea strengthened by the low level of genetic differentiation and phylogeographic structuring found within many partial migrant populations (Mun et al., 1999; Freeland et al., 2003; Raymond et al., 2013; Zhan et al., 2014).

How discrete migratory states within a population are maintained is unclear, but two hypotheses have been proposed (Chapman et al., 2011). One possibility is the attainment of an *evolutionary stable state*, where the fitness of each form is balanced by frequency-dependent selection. For example, in wing dimorphic insects where the more fecund flightless form is balanced by the colonizing abilities of the migrant morph (Roff, 1994; Zera and Denno, 1997). Alternatively, the fitness benefits of either morph may occur as a result of *conditional strategies*, were the decision to migrate is based upon gaining the highest fitness possible under certain circumstances and a balancing of fitness is not necessary (Chapman et al., 2011). The generally short life span of insect migrants and their higher reliance on favorable meteorological conditions for migration (Alerstam et al., 2011; Hu et al., 2016) highlights the importance for selecting the optimal strategy in any given situation. Migratory hoverflies, such as *E. balteatus*, for example, may migrate south to warmer climes (Wotton et al., 2019) but are also capable of sedentary overwintering behavior as adults, larvae, or pupae (Raymond et al., 2014a), an adaptation that presumably increases their fitness over attempting to migrate in unfavorable conditions (also see Vander Zanden et al., 2018).

The inheritance and phenotypic expression of migratory states has been investigated in both wing polymorphic (Fairbairn and Yadlowski, 1997; Roff et al., 1997) and monomorphic (Kent and Rankin, 2001) insects and interpreted in the context of the "threshold model": a quantitative genetic model for the evolution of polygenic, dichotomous traits (Roff, 1996). Under this model, a normally distributed trait, called the *liability*, underlies the expression of the migratory dimorphism and a *threshold* determines the developmental trajectory—in this case migrant or non-migrant. If the liability exceeds the threshold then the individual takes one path, say migration, if not it becomes sedentary. In the case of wing polymorphism, it is hypothesized that the liability for wing production may be governed by hormone profiles at a particular larval stage: in larvae where levels exceed the threshold (conceivably controlled by levels of hormone receptors among other factors) the flightless morph is formed (Oostra et al., 2011; Roff, 2011). An additional consideration is that threshold traits also vary with environmental factors such as temperature, photoperiod, and density (Hondelmann and Poehling, 2007; Guerra and Reppert, 2013). A more realistic model—the *environmental threshold model*—allows for both genetic variation, and for individual or environmental conditions to modify the threshold and the liability (Roff, 1994; Wikelski et al., 2006; Hallworth et al., 2018; see Pulido, 2011 for a full consideration of the model and its implications for partial migration) and therefore has the potential to provide a comprehensive framework for a deeper understanding of partial migration in insects.

## Ecological Implications of Partial Migration in Insects

Insects are the most abundant and speciose terrestrial migrants, with trillions of individuals undertaking movements annually (Holland et al., 2006; Chapman et al., 2015; Hu et al., 2016). Additionally, many migratory insect species are important agricultural pests (Drake and Gatehouse, 1995), or are beneficial—as pollinators or natural enemies (Wotton et al., 2019) or as food for other animals (Krauel et al., 2015; Warrant et al., 2016). Consequently, understanding the incidence and mechanisms involved in the regulation of partial migration in insect populations has significant implications for ecosystem functioning and species management. Models based on predator-prey dynamics and interactions with environmental conditions have been developed to study the ecosystem effects of partial migration in fish (Brodersen et al., 2008, 2011), and similar approaches may be considered for insects, particularly in the context of nutrient transfer between trophic levels and across landscapes. Furthermore, understanding the factors influencing the level of migration within populations may allow for the implementation of more realistic species management strategies.

## Future Directions and Gaps in Knowledge

Despite the deficiency of research investigating the mechanisms driving partial migration in insects, the phenomenon evidently occurs in numerous species, and there are exciting opportunities for research into the evolution and ecology of the phenomenon. Insects are excellent model systems; they are relatively small, easily maintained, and can be manipulated in a laboratory environment. The opportunity for identifying new partial migration study systems will be facilitated by the huge diversity of migratory insect species and their broad range of life histories.

Little is known about the influence of anthropogenic landscape change on partial migration in insect populations. There is evidence that landscape alterations can readily lead to an increase in the propensity for residency in migratory insects, usually in response to favorable conditions, such as the availability of food resources. For example, increased planting of tropical milkweed (*Asclepias curassavica*) in Florida has led to an increase in residency in monarchs, but residents suffer from increased parasitism compared to migrants (Satterfield et al., 2015). Urbanization can also increase the propensity for residency or overwintering through the provision of winter refugia or foraging resources, such as garden flowers. Luder et al. (2018) demonstrated that migratory hoverflies appeared earlier in the season in urban areas compared to agricultural areas, indicating that cities may provide favorable conditions for overwintering. Warming temperatures have also led to an increase in overwintering of migratory species in the UK, such as the red admiral butterfly (*Vanessa atalanta*), although much of the population still immigrates to the UK each spring (Sparks et al., 2005; Fox and Dennis, 2010). Fairly simple laboratory experiments could be used to shed light on whether warming or constant temperatures, or increased food constancy, influences the migratory propensity in wing-monomorphic insects.

Tracking the migratory behavior of insects in the field is difficult, primarily due to their small size and sheer numbers. Individual tracking of insects to determine migratory decisions has been hindered because the majority of species fall well below the body size required to carry active transmitters (Wikelski et al., 2006; Kissling et al., 2014; Knight et al., 2019). Consequently, many studies investigating insect migratory behavior which may be relevant to partial migration have been conducted in the laboratory, using proxy measures for migratory potential, such as flight duration and activity (Minter et al., 2018). Tethered flight experiments have proven useful for determining migratory tendency in a range of insect species (Dällenbach et al., 2018; Minter et al., 2018; Naranjo, 2019). However, the further miniaturization of individual tracking technology will provide exciting opportunities to understand the drivers of partial migration and the mechanisms that influence individual decision-making. The use of intrinsic markers, such as stable isotopes, has proven useful for elucidating the origin of migratory insects (Hobson et al., 2012; Flockhart et al., 2013; Hallworth et al., 2018) and is applicable to a range of species. Recent advances in molecular techniques, including metabarcoding of pollen carried on the bodies of insects also shows great promise (Suchan et al., 2019). Techniques using intrinsic markers, where the utility is not limited by the size of the insect, will likely prove key in understanding patterns of partial migration in many insect taxa.

## AUTHOR CONTRIBUTIONS

MM and KW wrote the first draft of the manuscript. All authors contributed to the development of ideas and writing of the manuscript.

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