# Migration in butterflies: a global overview

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## ABSTRACT

Insect populations including butterflies are declining worldwide, and they are becoming an urgent conservation priority in many regions. Understanding which butterfly species migrate is critical to planning for their conservation, because management actions for migrants need to be coordinated across time and space. Yet, while migration appears to be widespread among butterflies, its prevalence, as well as its taxonomic and geographic distribution are poorly understood. The study of insect migration is hampered by their small size and the difficulty of tracking individuals over long distances. Here we review the literature on migration in butterflies, one of the best–known insect groups. We find that nearly 600 butterfly species show evidence of migratory movements. Indeed, the rate of ‘discovery’ of migratory movements in butterflies suggests that many more species might in fact be migratory. Butterfly migration occurs across all families, in tropical as well as temperate taxa; Nymphalidae has more migratory species than any other family (275 species), and Pieridae has the highest proportion of migrants (13%; 133 species). Some 13 lines of evidence have been used to ascribe migration status in the literature, but only a single line of evidence is available for 92% of the migratory species identified, with four or more lines of evidence available for only 10 species – all from the Pieridae and Nymphalidae. Migratory butterflies occur worldwide, although the geographic distribution of migration in butterflies is poorly resolved, with most data so far coming from Europe, USA, and Australia. Migration is much more widespread in butterflies than previously realised – extending far beyond the well–known examples of the monarch *Danaus plexippus* and the painted lady *Vanessa cardui* – and actions to conserve butterflies and insects in general must account for the spatial dependencies introduced by migratory movements.

*Key words*: butterfly, butterfly migration ecology, conservation, insect movement, Lepidoptera, migratory butterflies, monarch, painted lady, seasonal movement.

CONTENTS

## I. INTRODUCTION

Migration is a widespread phenomenon among animals, particularly in vertebrates, insects, and marine invertebrates (Alerstam, Hedenström & Åkesson, 2003; Dingle, 2014). Animals that migrate range in size from tiny insects to blue whales, and comprise a remarkable proportion of animals worldwide, with that fraction constantly increasing as we learn more about animal movements (Cioc, 2009; Dingle, 2014). Distances travelled vary greatly, with some species making just local movements (Denno & Grissell, 1979; Denno *et al.*, 1980; Denno, Douglas & Jacobs, 1985), and others traveling thousands of kilometres between continents and even hemispheres (Alerstam *et al.*, 2003; Chapman, Reynolds & Wilson, 2015). From a conservation viewpoint, the often–vast geographic range sizes of migratory species might be assumed to protect them from extinction risk, yet migratory species can be acutely prone to threats occurring at key sites where they congregate at some point in the annual cycle (Koh & Sodhi, 2004; Wilcove & Wikelski, 2008; Flockhart *et al.*, 2015; Runge, 2015; Runge *et al.*, 2015; Stenoien *et al.*, 2016; Dhanjal−Adams *et al.*, 2017; Chowdhury *et al.*, 2020; Gao *et al.*, 2020). For example, habitat destruction and fragmentation, coupled with intense human predation led to the extinction of at least three formerly widespread and common migratory species: the Rocky mountain grasshopper *Melanoplus spretus*, the passenger pigeon *Ectopistes migratorius*, and Eskimo curlew *Numenius borealis* (Brower & Malcolm, 1991; Bucher, 1992; Hopkins, 2005; Harris *et al.*, 2012). Migratory connectivity between habitat patches may complicate the planning of conservation management activities, because it is necessary to account for spatial dependencies among sites when evaluating the benefits of alternative conservation actions (Brower & Malcolm, 1991; Martin *et al.*, 2007; Miller *et al.*, 2012; Iwamura, Fuller & Possingham, 2014; Flockhart *et al.*, 2015; Dhanjal−Adams *et al.*, 2017).

Migration enables individuals to find and occupy more favourable habitats as or before the current habitat deteriorates, often (although not always) on a regular temporal schedule. Individuals exhibit morphological, physiological, and behavioural traits that enable migration to occur (Berthold, 1999; Åkesson & Hedenström, 2007). For example, many migratory animals have an internal 'biological clock' (Gwinner, 1996) that schedules the various components of the migration (Liedvogel, Åkesson & Bensch, 2011). To find their species– or population–specific seasonal quarters, migrating animals need to combine elements of temporal and spatial information into a spatiotemporal migration programme (Åkesson & Hedenström, 2007).

Insect migration is much less well studied than migration in birds and other vertebrates, despite its potentially huge importance to ecological resource flows and ecosystem services globally (Hu *et al.*, 2016; Menz *et al.*, 2019; Wotton *et al.*, 2019; Satterfield *et al.*, 2020). Migration occurs in all major insect taxonomic groups, although its prevalence varies markedly among species, even within closely related clades (Drake & Farrow, 1988; Dingle, 2001; Dingle *et al.*, 2005). Migratory species occur in all functional groups of insects: pollinators, herbivores, predators in the broad sense, decomposers, and of course, pests – insects that are vectors of human, livestock and plant diseases, as well as those that directly damage crops (Walther *et al.*, 2002; Dingle, 2006, 2009; Reynolds, Chapman & Harrington, 2006). Migration is the key process in the ecology and population dynamics of many insect species, yet perhaps as a consequence of their small size and general lack of mass aggregation in comparison with vertebrates, the migration of insects remains mostly unnoticed and, with only a few exceptions, poorly studied (Chapman *et al.*, 2015; Gao *et al.*, 2020; Satterfield *et al*., 2020). Yet new technologies and the advent of mass–participation citizen science are beginning to document the large–scale movements of insects in ways that have hitherto been unavailable (Stefanescu *et al.*, 2013; Cohen *et al.*, 2019; Knight *et al.*, 2019; Juhász *et al*., 2020). Here we review and synthesise what is known about migration in butterflies, and outline some of the key information gaps.

Butterflies are one of the better–studied groups of insects; generally, there is a good understanding of their ecology, and we know that the degree of connectivity between fragmented populations is critical to effective conservation (Brower & Malcolm, 1991; Hanski & Thomas, 1994; Baguette, Petit & Quéva, 2000; Hanski, Alho & Moilanen, 2000; Koh & Sodhi, 2004; Gao *et al*., 2020; Chowdhury *et al*., 2021). About 19% of all bird species migrate (Kirby *et al*., 2008; Somveille *et al.*, 2013), but perhaps surprisingly, the number of migratory butterfly species, often dubbed the 'birds of the insect kingdom', remains unknown. There are reports of migration across various butterfly families, suggesting that at least a few hundred species might migrate, but given the difficulty of studying the phenomenon it is plausible this is vastly underestimated. Williams (1930) summarised all existing research at the time of writing and reported 217 migratory butterflies. This work is now 90 years old, and there is no recent comprehensive review of the prevalence of butterfly migration.

Here we conduct such a review, collating and summarising published descriptions of butterfly migrations globally, highlighting key aspects of the migration phenomenon in butterflies, analysing previous findings, and pointing out major knowledge gaps. We ascertain, to the extent that current knowledge allows, and based on multiple lines of evidence, which butterfly species are migratory, provide lists by zoogeographic region, show where and how butterfly migration has been studied, and evaluate potential drivers of migration. We hope this work will stimulate greater scrutiny and assessment of migratory movements made by butterflies, with a view to improving ecological understanding and planning systematically for butterfly conservation.

## II. BUTTERFLY MOVEMENTS

Butterflies are relatively large–bodied for insects, reasonably well described taxonomically, often colourful, and usually diurnal (compared with the much larger number of moth species), and they are more likely to be observed and recorded than any other insect group (New, 1997; Hickling *et al.*, 2006). Butterflies are known to exhibit the full range of movement types, from extreme sedentariness (Ehrlich, 1986; Walther *et al.*, 2002) to some of the longest–distance insect migrations, in which individuals cover thousands of kilometres or perform complex intergenerational relays over similar distances (Stefanescu, 2001; Mouritsen *et al.*, 2013b; Stefanescu *et al.*, 2013; Runge *et al.*, 2014). Some *Euphydryas* checkerspot butterflies are extremely sedentary, remaining restricted to localised colonies and with only short–distance dispersal (Ehrlich & Gilbert, 1973), although movement patterns vary markedly among species (Brown & Ehrlich, 1980), and among populations of the same species (Gilbert & Singer, 1975). Edith’s checkerspot *Euphydryas editha* is the least vagile checkerspot butterfly in the western USA, although it too disperses when disturbed or when habitat conditions become suboptimal (Ehrlich, 1986). By contrast, monarchs *Danaus plexippus* travel about 5000–6000 km to complete their annual migration over 3–5 generations (Brower, 1995), and regularly move between patches of larval food plant during the breeding season (Grant *et al.*, 2018), although they frequently become 'sedentary' after colonising small islands (Freedman *et al*., 2018). Painted ladies *Vanessa cardui* migrate more than twice as far (up to about 15,000 km) in round–trip migrations from Northern Europe to West Africa over at least 6–7 generations (Pollard *et al.*, 1998; Stefanescu *et al*., 2013; Talavera *et al*., 2018).

Butterfly movements fall into two main types: (1) flying within, or (2) going beyond their local habitat or some other circumscribed area (equivalent to the home range of vertebrates). Butterflies showing the latter type of behaviour are often considered migrants (Dingle, 1996, 2009, 2014; Nesbit *et al.*, 2009). The major difference between migrant and non–migrant individuals is that the former generally do not get distracted by appetitive cues such as food items and particularly sexual signals (Dingle, 1978; Chapman & Drake, 2016), although migratory butterflies often pause their journey to collect nectar and then resume flight towards their destination (Dingle, 2009). In vertebrates, migration is usually taken to mean an outward and return journey by the same individual (Dingle & Drake, 2007), yet due to their short lifespan, the pattern in butterflies is for successive generations to execute long–distance directional movement resulting in an overall change in the distribution of a population in response to an environmental cue (Baker, 1969; Alerstam *et al.*, 2003; Milner–Gulland, Fryxell & Sinclair, 2011).

The definition of migration varies from author to author, but a common thread among most definitions is that individual behaviour can be used to differentiate migration from other movement behaviours (Dingle & Drake, 2007). Kennedy (1985, p. 8 ) proposed a widely used definition based upon behavioural aspects: “Migratory behaviour is persistent and straightened–out movement effected by the animal’s own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station–keeping responses but promotes their eventual disinhibition and recurrence”. Not all migrants will show the same suite of characteristics, and flexibility around characterising and diagnosing the phenomenon is needed (Kennedy, 1985).

In comparison with many vertebrates, migrations in butterflies may seem rather atypical, which has led to a diversity of viewpoints on what constitutes migration in butterflies. In this review, we adopt the broad behavioural definition quoted above, recognising that it can only be applied with certainty to a small number of species. However, we argue that this reflects the lack of research (and the resultant lack of data and knowledge) on these butterflies, rather than a failure of the definition itself. As pointed out by Gatehouse (1997), there remains a lack of research on the behavioural and physiological aspects of migration with respect to Kennedy’s (1985) definition. We hope that our review will stimulate such research to determine whether particular species or individuals are in fact migrants. Some movement ecology researchers, particularly those with experience of ‘classic’ vertebrate migration systems might consider some of the butterflies we classify as migratory as better classified as dispersive species; however, we adopt this broader view to establish a first framework for future studies of butterfly migration.

Partial migration, whereby part of any population migrates while the rest remains resident, (Chapman *et al*., 2011*a*; Malcolm & Slager, 2015; Slager & Malcolm, 2015; Ruiz Vargas *et al*., 2018; Menz *et al*., 2019) is likely to be common in butterflies. For example, Vander Zanden *et al*. (2018) collected 33 monarchs in south Florida; isotopic analysis showed that 48% of the individuals originated from further north (i.e. they were recent immigrants), while

52% had developed locally (i.e. they were residents). As butterflies are generally short–lived with rapid generation times, the migratory cohorts are more likely to be separated temporally rather than spatially (as is typical of vertebrate partial migrants; Chapman *et al*., 2011*b*), and such situations have been termed 'sequential partial migration' (Ruiz Vargas *et al*., 2018). This category of partial migration may well prove to be the most common type of migration exhibited by butterflies. The key to resolving such issues will be to approach the study of migration from more than just observations of numbers flying past a fixed location, the main approach used to categorise migration in most species to date (see Section IV).

## III. LITERATURE SEARCH

We searched *Google Scholar*, *PubMed*, and *Web of Science* to determine which butterfly species have been considered migratory according to at least one or more lines of evidence. Initially, we used 'butterfly migration' and 'migratory butterflies' as search terms in *Google Scholar* and carefully scanned the first 1000 search results for relevant papers. We then searched *Google Scholar* for specific information on the migratory status of each species (*X*) identified during the initial search using the search term '*X* migration'. In *PubMed*, the search terms 'butterfly migration' and 'migratory butterflies' yielded a total of 228 journal articles. A *Web of Science* search using 'TS=(Butterf* AND migr*)', yielded 1,297 publications. In both cases we followed up each suspected migratory species with a specific search. We also checked the bibliography of each article to identify other relevant literature. Many authors publish on butterfly migration in local journals or newsletters (e.g. *Atalanta*, *Phygea*, *Bulletin of the Allyn Museum*, and *Journal of the Bombay Natural History Society*), yet during our literature search using the above search engines, we rarely located relevant work in these journals. Therefore, we carefully checked all issues of these publications to locate butterfly migration–related publications. Eventually, during our literature search in both Google Scholar and Web of Science, we found repetition of the same literature and started to come across hundreds of non–relevant works, suggesting we were approaching saturation, at least of the readily available literature. Together, from all sources we identified 422 articles, 36 books, 9 book chapters, 2 book reviews, 10 letters, 3 meeting abstracts, 16 notes, 43 review articles, 23 web articles, 5 theses and 9 proceedings (marked with asterisk (*) in the reference section). Our searches were conducted up to December 2019 and we primarily considered articles written in English; however, if we identified relevant publications in other languages, these were translated.

## IV. EVIDENCE FOR MIGRATORY STATUS

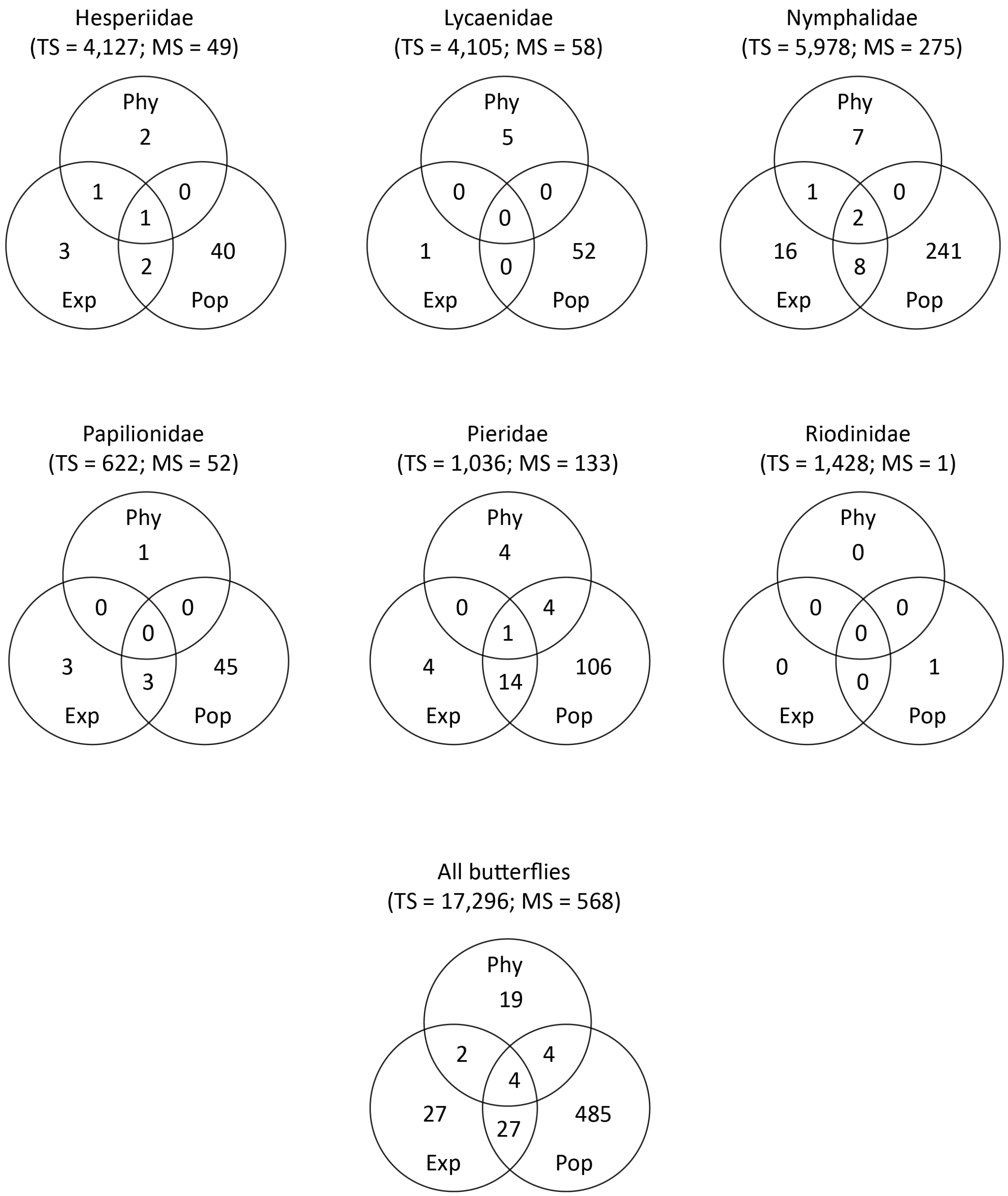
We focused on the primary literature on observations of butterflies migrating or for specific instances in which migratory behaviours were inferred, and built a list of methods that have been used to ascribe migratory status (Table 1). These fell into the three major groups of experimental, physiological and population evidence. General assertions that a species was migratory were not sufficient to consider that migration had been proved for a particular species. Instances of directional flights in which individuals appeared undistracted strongly suggest that the butterflies were migrating, and were included (Dingle, 2001; Dingle & Drake, 2007). In other instances where there was no mention of individual behavioural characteristics, migration could still be inferred if there was documentation of butterflies occurring in the absence of larval food plants, performing nomadic or seasonal movements, where large numbers were recorded roosting or imbibing nectar, and where there was evidence of formation of overwintering aggregations at specific sites that are strongly suggestive or indicative of migration (see Table S1 for full details).

Table 1. Methods that have been used to attribute migratory behaviour to butterflies with example references for each. See Table S1 for full details of species studied using each of these methods.

| **Evidence (broader categories)** | **Evidence (specified)** | **Description** | **References** |
|---|---|---|---|
| Physiological | Larvae are incapable of developing due to unfavourable seasonal climate | The environment is not suitable for the larvae to complete development | Clements (2012) |
| Physiological | Extended pre-oviposition period | Female butterflies delayed egg maturation, suggesting time available to migrate rather than reproduce | Johnson (1963) |
| Physiological | Larval food plant absent | Larval food plants were absent where the butterfly was seen, suggesting they were flying through and not breeding | Braby (2005) |
| Physiological | Breeding population not established | Butterfly recorded in an area where there was no breeding record | Braby (2000) |
| Experimental | Mark–release–recapture | Marked individuals displaced away from mark site and recaptured along 'flight path'; marked individuals recaptured a long way from marking site along flight path | Urquhart (1960); Urquhart & Urquhart (1976); Matter *et al.* (2004) |
| Experimental | Trap catches | A trap built along the migratory route was used to catch migrant butterflies and identify their migratory direction | Walker (1985*b*) |
| Experimental | Tethered flight measurements | Used to establish orientation and potential displacement under various conditions | Mouritsen & Frost, (2002); Reppert *et al.* (2004); Mouritsen (2018) |
| Experimental | Amplified fragment length polymorphism (AFLP) | The occurrence of distinct genetic types can be used to understand whether long-distance movements occur, and to link breeding and non-breeding grounds. | Brattström *et al.* (2010*a*, *b*) |
| Experimental | Radar observations | Provide direct records of insects flying at high altitude | Drake & Farrow (1985); Chapman *et al.* (2011*b*) |
| Experimental | Flight in beneficial compass direction | Establish vanishing angles, direction of movement, orientation, etc. | Srygley (2001); Srygley & Oliveira (2001); Srygley *et al.* (2006) |
| Experimental | Stable isotopes | Stable isotope (dD) used to determine probable geographic origins of migrants | Wassenaar & Hobson, (1998); Brattström *et al.* (2010*a*, *b*). |

| **Evidence (broader categories)** | **Evidence (specified)** | **Description** | **References** |
|---|---|---|---|
| Experimental | Maintaining constant compass course by using wind Drift Compensation | Flights were compensated with respect to wind speed/direction | Srygley (2001); Srygley & Dudley (2008) |
| Population evidence | Mass movement | Many butterflies moving in the same direction at the same time, and that were apparently undistracted by appetitive cues | Shapiro (1982, 1986); Stefanescu (2001); Burwell *et al.* (2011) |

We identified 13 lines of evidence that have been used to diagnose butterfly migration and grouped them into three broader categories: experimental (8 lines of evidence), physiological (4), and population evidence (1) (Table 1). For each species, we collated sources that provided evidence of migration status, categorised into one of these 13 types (Table 1). The number of methods to assess migratory status of a butterfly varied markedly (Table S1). We found only a single line of evidence for 92% of species classified as migratory (521 of the 568), two or three lines of evidence for 36 species, and four or more lines of evidence for only 10 species (all in Pieridae and Nymphalidae). We found a further 23 species where authors asserted that a species was migratory but did not provide any evidence; we do not consider that migration has been proved in these species and exclude them from this review. It is clear that most work on butterfly migration has focused primarily on a small suite of species, with only 46 species having more than one line of evidence for migration in the literature. There remains a great deal of work to do on the migration of most butterfly species. Although direct experimental work is the best indicator of migratory behaviour, most authors used changes in distribution (population evidence), or records of behaviour (Fig. 1) to infer migration. For example, many authors consider a butterfly to be a migrant if mass movement has been noted; this line of evidence accounts for the diagnosis of migration in more than 90% of cases. Analysis of amplified fragment length polymorphism (AFLP) or similar approaches has been used to determine migratory status only for a single species (red admiral *Vanessa atalanta*) despite the fact that this method is commonly used to determine population structure and migration among bird species (Bensch, Åkesson & Irwin, 2002; Bensch & Åkesson, 2005; Brattström, Åkesson & Bensch, 2010*a*; Brattström *et al*., 2010*b*). Flight chamber experiments involving tethered flight have been used for only five species (see Table S1).



Hesperiidae (TS = 4,127; MS = 49)

Lycaenidae (TS = 4,105; MS = 58)

Nymphalidae (TS = 5,978; MS = 275)

Papilionidae (TS = 622; MS = 52)

Pieridae (TS = 1,036; MS = 133)

Riodinidae (TS = 1,428; MS = 1)

All butterflies (TS = 17,296; MS = 568)

**Fig. 1.** Methods used to ascribe migratory status to butterflies. Here, TS = Total identified species, MS = Total recorded migratory species, Phy = physiological evidence; Exp = experimental evidence; Pop = population evidence. The species number beside each family is the total number of species in the world and numbers in the circles indicate how many

species have been diagnosed as migratory with that particular method or combination of methods. The total number of butterflies in each subfamily is derived from an online data repository (https://www.learnaboutbutterflies.com/World%20Census.htm). Note that many species have been diagnosed as migratory based on only a single category of evidence.

## V. PREVALENCE OF MIGRATION

In total, we found evidence for migration in 568 species of butterflies belonging to 221 genera, from 21 subfamilies, across all six major families (see Table S1). At the family level, Pieridae had the greatest proportion of migrants, with 13% (133 species) being documented as migratory, followed by Papilionidae (8%; 52 species), Nymphalidae (5%; 275 species), Lycaenidae (1%; 58 species), Hesperiidae (1%; 49 species), and finally only one of the 1428 species in the Riodinidae (Fig. 1). At the sub–family level, Libytheinae (Nymphalidae) contains the highest proportion of butterfly migrants (nine species, 53%), while Pierinae (Pieridae) contains the highest number of migrants (80 species, 11%). Interestingly, migrants appear more prevalent in smaller subfamilies (Fig. 2), but it is unclear whether this represents differences in the extent to which the different subfamilies have been studied or genuine differences in the biological prevalence of migration in some phylogenetic clades.

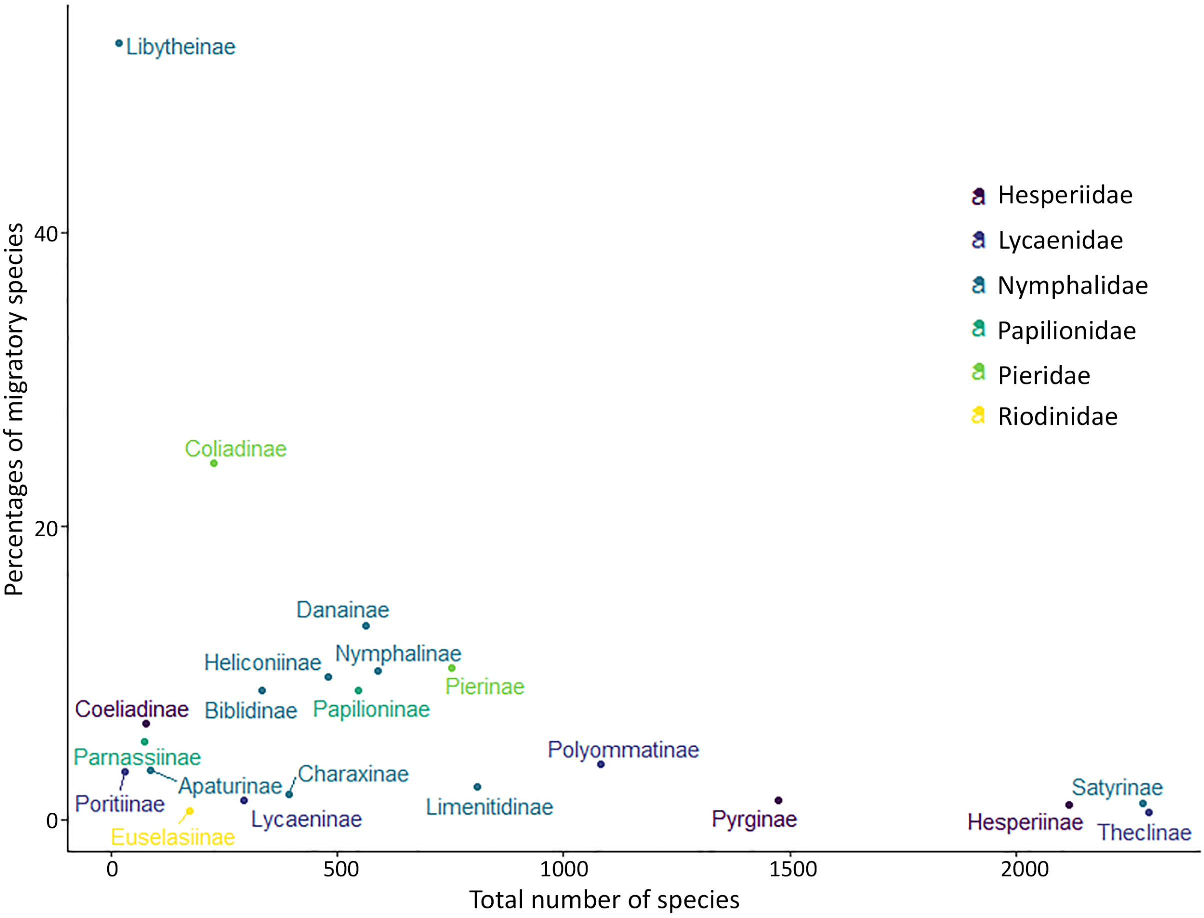


**Fig. 2.** Prevalence of migratory species among butterfly subfamilies. The total number of butterflies in each subfamily is from https://www.learnaboutbutterflies.com/.

It is clear that butterfly migration is a widespread global phenomenon, although the number of recorded migrants varies markedly from continent to continent and from region to region (Fig. 3). While only 3% of described butterfly species globally have been diagnosed as migratory to date (Fig. 1), the proportion varies markedly from one zoogeographic region to another. Migratory butterflies are mostly recorded from the Holarctic (Nearctic and Palaearctic) region (12% in each); while in the Neotropical and Afrotropical regions together, around 5% of the butterflies are migratory, 7% from the Australian region, and roughly 8%

are migratory in the Oriental region (Fig. 3). These results are likely to reflect substantial regional bias in research attention and many migrants might remain undetected.

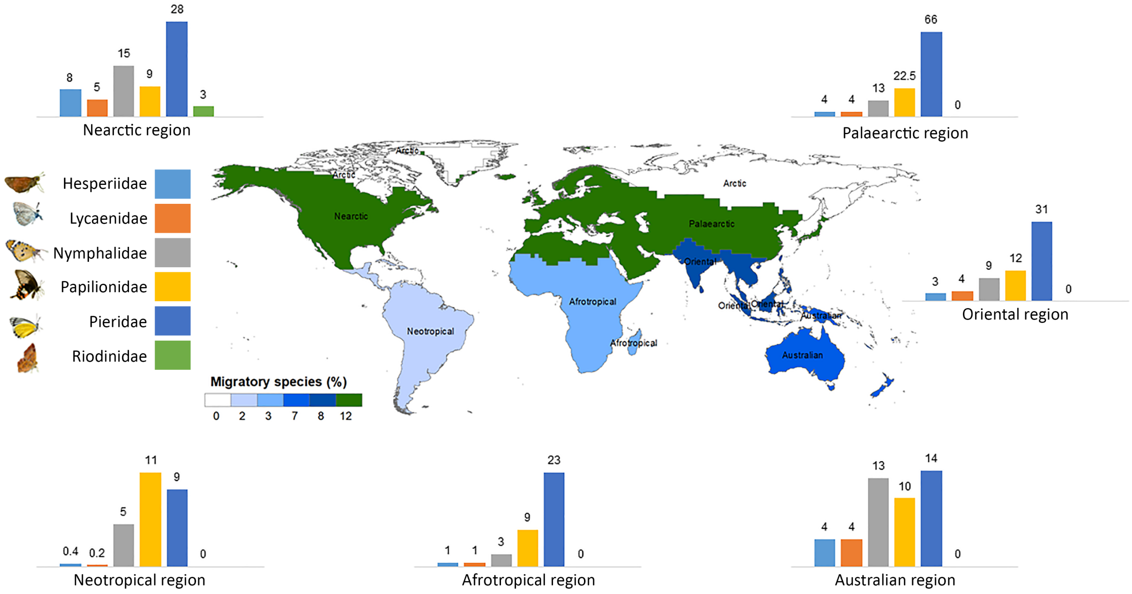

8
5
15
9
28
3
Nearctic region
4
4
13
22.5
66
0
Palaearctic region
Hesperiidae
Lycaenidae
Nymphalidae
Papilionidae
Pieridae
Riodinidae
Arctic
Arctic
Nearctic
Arctic
Palaearctic
Oriental
Oriental
Oriental
Australian
Afrotropical
Afrotropical
Neotropical
Australian
3
4
9
12
31
0
Oriental region
Migratory species (%)
0
2
3
7
8
12
0.4
0.2
5
11
9
0
Neotropical region
1
1
3
9
23
0
Afrotropical region
4
4
13
10
14
0
Australian region

**Fig. 3.** Prevalence of butterfly migration across the world. Colours on the map indicate the percentage of all described butterflies for each zoogeographic region that are considered migrants. The bar charts indicate the percentage of described butterflies in each zoogeographic region that are considered migrants, separated according to family.

Migratory butterflies were recorded from all continents except Antarctica (which has no butterflies). Most butterfly migration was recorded from predominantly tropical countries (e.g. Australia, India, and Sri Lanka had the highest total numbers of migratory species), indicating that this phenomenon is not restricted to strongly seasonal high latitudes. However, when expressed relative to the total butterfly species present, higher latitude temperate or cooler countries have higher proportions of migratory species: 12% of Palaearctic butterflies are migratory compared to 3% of the butterflies from the Afrotropical region (Fig. 3). In an analysis of the distribution of Australian migratory and non–migratory butterflies, Dingle *et al*. (2000) found migrants to be more common in arid areas.

The geographic spread of species that migrate varied among families. In the Papilionidae, migratory species were mostly documented in the Palaearctic (23%), while for the Nymphalidae migrants were most common in the Nearctic (15%). In all five regions globally, migration was most prevalent in the Pieridae, while only one species in the Riodinidae was reported as a migrant (from the Palaearctic) (Fig. 3). Although 13% of the world's pierids are migratory, the proportions are substantially higher in some regions (66% of Palaearctic pierids, 31% of Oriental pierids, and 28% of Nearctic pierids are migratory) and negligible in others (Fig. 3).

There was a clear disparity between documentation of migration, and the global distributions of species in which migration has been documented. This presumably indicates either a spatial bias in where migration is studied, or that these species do not migrate in all parts of their geographic distribution. Records from Afrotropical and Neotropical regions were scarce. In addition, we could only find evidence for a single migratory species of Riodinidae (*Euselasia euboea*; Williams, 1930). Riodinid butterflies are generally restricted to specific microhabitats and may be spatially rare with low population densities, even where they have wide distributions (DeVries, Chacon & Murray, 1992; Campbell & Pierce, 2003; Siewert *et al.*, 2014; Espeland *et al.*, 2015). It would be interesting to further investigate the migration of Riodinidae since we found only one reference (*Euselasia euboea*; Williams, 1930) documenting an instance of migration in this family. Future studies could investigate whether there are particular ecological or genetic characteristics that constrain riodinids in terms of migration.

Migration has been observed across the geographic range of several widespread species, with up to 30% of butterflies recorded as migrants from more than one region. *Vanessa cardui* was recorded as a migrant in six regions; migration of *Hypolimnas misippus*, *Ascia monuste*, and *Pieris rapae* has been recorded from five regions; twelve species (*Belenois aurota*, *Colias croceus*, *Colias hyale*, *Danaus chrysippus*, *Danaus plexippus*, *Hypolimnas bolina*, *Junonia orithya*, *Lampides boeticus*, *Libytheana carinenta*, *Nymphalis antiopa*, *Pieris brassicae*, and *Vanessa atalanta*) migrate in four regions.

For 24 species, we found inconsistent records: one author specifically noting sedentariness in contrast to another author considering the same species to be a migrant elsewhere (Table 2). For example, both *Heliconius erato* (Turner, 1971) and *H. ethilla* (Ehrlich & Gilbert, 1973) have been described as sedentary, although *H. ethilla* and other *Heliconius* species have been recorded elsewhere as taking part in large–scale migrations (Williams, 1930; Beebe, 1949a, b; Beebe, 1950*a*,*b*).

Table 2. List of species that have been recorded as both migratory and non-migratory/ resident.

| **Species** | **Recorded as migratory** | **Recorded as non-migratory** |
|---|---|---|
| *Acraea terpsicore* | Williams (1927, 1930); Larsen (1988); Dunn & Petrie (2017) | Bhaumik & Kunte (2018) |
| *Aporia crataegi* | Williams (1930); Baker (1969); Larsen (1975); Beshkov (1996*a*); Bolotov *et al.* (2013) | |
| *Araschnia levana* | Bolotov *et al.* (2013) | Parmesan *et al.* (1999) |
| *Argynnis adippe* | Baker (1969) | Parmesan *et al.* (1999) |
| *Celastrina argiolus* | Williams (1930); Williams *et al.* (1942); Baker (1969); Cook *et al.* (2001) | Parmesan *et al.* (1999) |
| *Colias eurytheme* | Shapiro (1973, 1980*a*); David (1982); Ferris (1989, 1993); Fleishman *et al.* (1999) | Ferris (1988) |
| *Colias philodice* | Fenton (1919); Williams (1930); Clark (1931) | Ferris (1988) |
| *Colotis fausta* | Williams (1930); Larsen (1975, 1984, 1986) | Larsen (1987) |
| *Cupido argiades* | Williams (1938); Williams *et al.* (1942); Baker (1969); Vermandel & Vliegenthart (2014) | Parmesan *et al.* (1999) |
| *Danaus chrysippus* | Evershed (1910); Williams (1930); Williams (1938); Dell (1977); Larsen (1984); Braby (1988); Harris (1988); Dingle *et al.* (1999); Smith (2014) | Bhaumik & Kunte (2018) |
| *Danaus gilippus* | Williams (1930); Miller (1985); Simon & Miller (1986); Gibo (1993); Haber (1993) | Brower (1995) |
| *Euphydryas editha* | Harrison (1989) | Gilbert & Singer (1975) |
| *Euploea midamus* | Williams (1930); Chan (2004); Wong *et al.* (2004); Yiu (2009) | Bhaumik & Kunte (2018) |
| *Euploea mulciber* | Williams (1930); Wang & Emmel (1990); Orr (1992); Chan (2004); Wong *et al.* (2004); Yiu (2009) | Bhaumik & Kunte (2018) |
| *Eurema herla* | Williams (1930) | Braby (2005*a*) |
| *Eurema laeta* | Williams (1927, 1930, 1938) | Braby (2005*a*) |
| *Heliconius ethilla* | Williams (1930); Beebe (1950*a*) | Ehrlich & Gilbert (1973) |
| *Maniola jurtina* | Williams *et al.* (1942) Baker (1969) | Parmesan *et al.* (1999) |
| *Nymphalis californica* | Williams (1930); Shapiro (1982, 1986) | Shapiro (1976) |
| *Parnassius apollo* | Nakonieczny *et al.* (2007) | Parmesan *et al.* (1999) |
| *Parnassius mnemosyne* | Välimäki & Itämies (2003); Vlasanek *et al.* (2009); Bolotov *et al.* (2013) | Parmesan *et al.* (1999) |

| Species | Recorded as migratory | Recorded as non-migratory |
|---|---|---|
| *Polygonia c-album* | Baker (1969); Beshkov (1996*a*, *b*) | Parmesan *et al.* (1999) |
| *Pyronia tithonus* | Cook *et al.* (2001) | Parmesan *et al.* (1999) |
| *Tirumala septentrionis* | Williams (1927); Evershed (1910); Fisher (1945); Chan (2004); Larsen (1987, 2004); Yiu (2009); Ramesh *et al.* (2012) | Bhaumik & Kunte (2018) |

## VI. STUDYING BUTTERFLY MIGRATION

Migration syndromes were first recorded in the early–19th century by Charles Darwin during his famous journey on the Beagle (Darwin, 1903), followed in the early 20th century by other notable contributions (Hayward, 1925, 1953, 1967; Williams, 1957, 1958). Since then, observing and recording migrating butterflies has become popular among professional and amateur lepidopterists worldwide, and now hundreds of species are known to be migratory (Fig. 4).

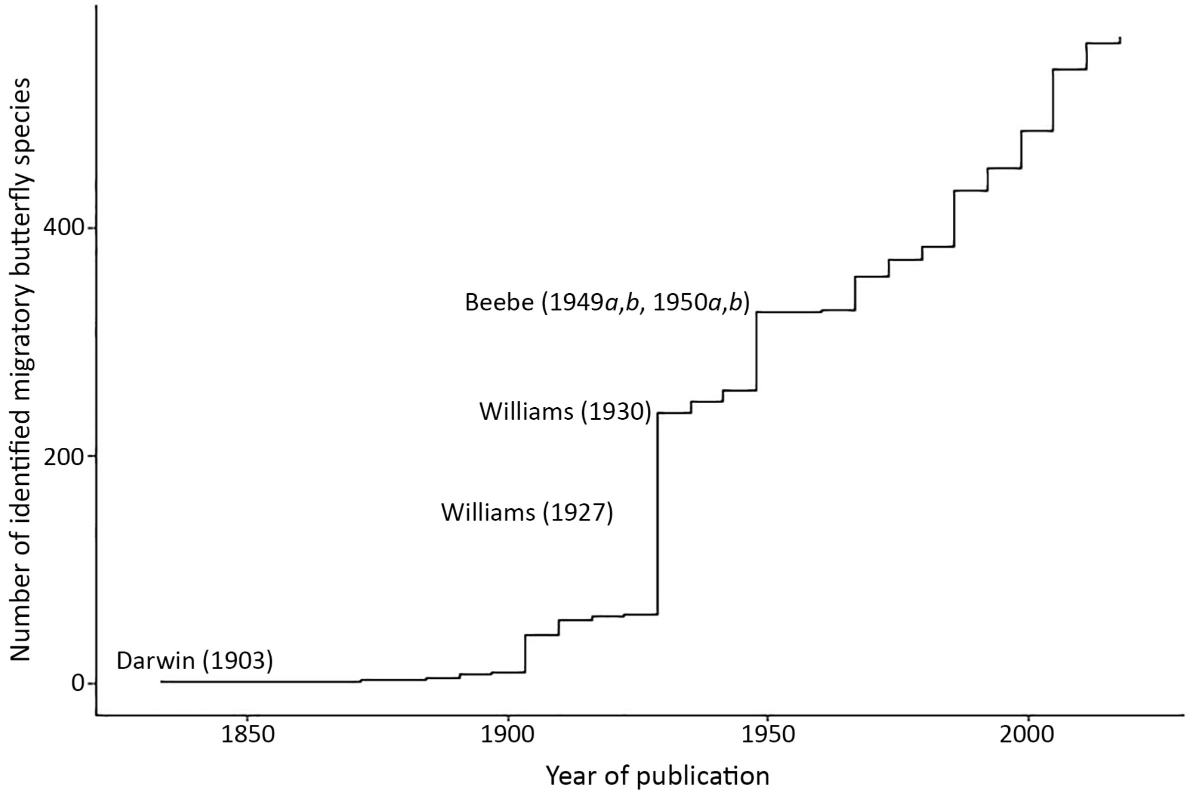


**Fig. 4.** Cumulative number of butterfly species documented as being migratory. Key publications responsible for rapid increases in the list of known migrants are noted.

Discoveries of migratory butterflies have increased steadily in recent decades (Fig. 4), yet much of this research effort is focused on a very small number of species (notably *Danaus plexippus*, *Vanessa cardui*, and *Vanessa atalanta*) with little work on the majority of species, substantially biasing knowledge of migration among butterflies globally. Nearly 55% of the studies we located were focused on just two species, *D. plexippus* (215 studies) and *V. cardui* (124 studies). We found only one or two research studies for 76% of migratory butterflies, with more than 10 publications for only 5% of butterflies recorded as migratory. For less–studied species, most authors used relatively weak lines of evidence to diagnose migration, such as records of mass movement, or nomadic behaviour. Very few studies have reported physiological (5%), and experimental (11%) lines of evidence (Fig. 1).

Thaxter (1880) was the first to describe the overwintering sites of various butterflies including monarchs, along the California coast. However, it took nearly a century to elucidate the monarch migration cycle fully (Malcolm *et al.*, 1993; Brower, 1995) and to identify their major overwintering site in the Transvolcanic Mountains of central Mexico following nearly 38 years of study, including 24 years of tagging studies (Urquhart & Urquhart, 1976). Until the 1960s, most research on butterfly migration was experimental, but in the early 1960s, C.G. Johnson investigated differences in life–history traits between migratory and non–migratory butterflies. Johnson found that migratory females start their flight before ovarian development (i.e. they are sexually immature), that they usually increase in body mass prior to migration, and that they possess longer forewings (Johnson, 1963, 1969). Genetic techniques were first used to study migration in the mid–1970s, when Eanes & Koehn (1978) collected summer migrant monarchs from the USA and Canada, and used electrophoretic alleles at six enzyme loci as genetic markers to study the genetic structure of the population. They found significant allele frequency variation between migratory and non–migratory individuals (Eanes & Koehn, 1978). Malcolm *et al.* (1993) used the presence of plant–derived cardenolides in monarch butterflies to describe spring migration in relation to the temporal and spatial distribution of about 130 species of their larval host plant, milkweed (*Asclepias* spp.). In recent decades, there has been rapid improvement in the use of genetic tools to uncover patterns of migratory connectivity (Sauman *et al.*, 2005; Dingle, 2006; Zhu, Casselman & Reppert, 2008; Zhan *et al.*, 2014; Reppert & de Roode, 2018), specialised radar to detect high–flying migratory butterflies (Chapman *et al.*, 2010; Stefanescu *et al.*, 2013; Chapman & Drake, 2016), isotopic tools to track the origin of migratory butterflies (Wassenaar & Hobson, 1998; Flockhart *et al.*, 2013, 2015), and tethered flight studies to identify migratory orientation (Mouritsen & Frost, 2002; Reppert, Zhu & White, 2004; Nesbit *et al.*, 2009).

## VII. CONSERVING MIGRATORY BUTTERFLIES

Migratory species can be acutely vulnerable to threats, since they depend on a series of habitats throughout their migration route (Runge *et al*., 2014). Yet, reports on the conservation status of migratory butterflies are sparse except for monarchs (Brower *et al.*, 2012; Flockhart *et al*., 2015; Semmens *et al.*, 2016; Agrawal & Inamine, 2018; Agrawal, 2019). While European populations of some well–known migratory butterflies are considered stable [e.g. painted lady *V. cardui*, red admiral *V. atalanta*, and clouded yellow *Colias croceus* (Fox *et al.*, 2015)], in North America there is very good evidence of a strongly declining population trend in the monarch.

In North America, the monarch butterfly is declining so rapidly (80% over the last decade) that it may soon lead to the demise of this world–famous migration (Brower & Malcolm, 1991; Semmens *et al.*, 2016). Several factors including loss of larval food plants (milkweed *Asclepias* spp.) and nectar resources, degraded overwintering habitats, climate change, influence of invasive milkweeds and natural enemies, global wind patterns, artificial light, habitat fragmentation, pathogens, agriculture and genetically modified crops, and declining fecundity, etc., have all been implicated, demonstrating the complexity of diagnosing and reversing declines in populations of migratory species (Malcolm *et al.*, 1993; Brower *et al.*, 2012; Oberhauser, Nail & Altizer, 2015; Oberhauser *et al.*, 2017; Pleasants *et al.*, 2016, 2017; Stenoien *et al.*, 2016; Thogmartin *et al.*, 2017; Malcolm, 2018; Agrawal, 2019; Freedman *et al.*, 2020).

The abundance and diversity of butterflies is controlled to a great extent by the presence and absence of food plants (Zalucki & Suzuki, 1987; Brower *et al.*, 2012; Batalden, Oberhauser & Peterson, 2014; Robertson, Zalucki & Paine, 2015; Pleasants & Oberhauser, 2017; Chowdhury *et al.*, 2020, 2021), and a landscape–level reduction of host plants can cause huge impacts on migrants (Zalucki & Kitching, 1982; Zalucki & Suzuki, 1987; de Roode *et al.*, 2008; Dyer & Forister, 2016; Pleasants & Oberhauser, 2017). For example, in North America, the use of genetically modified crops can impact insect–herbivore relationships and interspecific competition with other weeds (Rehfeldt *et al.*, 2012). The availability of herbicide–tolerant crops has changed agricultural practices from conventional tillage to no–till, and milkweed has been extirpated in soy and corn fields by the use of large quantities of glyphosate (Zalucki, Brower & Alonso, 2001). Genetically modified maize plants expressing crystalloproteins from the soil bacterium *Bacillus thuringiensis* (Bt) that are toxic to lepidopteran larvae can increase monarch larval mortality by 44% (Losey, Rayor & Carter, 1999). Field experiments showed that Bt maize pollen deposited on potted plants is toxic to first–instar monarch larvae (Jesse & Obrycki, 2000). Currently, the general consensus is that the risk to monarchs from Bt pollen is low because the fraction of the population exposed is small (Sears *et al.*, 2001).

Concern is increasing regarding the use of neurotoxic neonicotinoids, such as imidacloprid seed treatments, to control arthropod pests (Malcolm, 2018). The insecticide is present in the pollen and nectar of treated plants (Cresswell, 2011), leading to lethal to sub–lethal doses of imidacloprid being taken up by nectar–feeding butterflies (Stenoien *et al.*, 2016; Malcolm, 2018). Smoke from agricultural fires near the Mexican overwintering site for monarchs, which drifts up the mountainsides into the colonies of hibernating butterflies, is considered an ominous threat (Brower & Malcolm, 1991). When the air temperature is near the flight threshold, smoke causes frenzied flight, but if the temperature is below this threshold, the butterflies drop to the ground with a substantially increased predation risk (Brower, 1977; Calvert, Hedrick & Brower, 1979; Glendinning, Mejia & Brower, 1988; Brower & Malcolm, 1991).

The availability of nectar plants also depends on precipitation; thus, drought will influence the presence of nectar for migratory butterflies such as monarchs (Stenoien *et al.*, 2016; Thogmartin *et al.*, 2017). For example, monarchs feeding on irrigated *Liatris mucronata* were able to store up to 80mg of lipids in their body tissues, whereas those feeding on the drought–stressed *Verbesina virginica* plants could only store half this amount (Brower *et al.*, 2015). In addition, fire suppression can play a key role in the abundance of nectar resources (Rudolph *et al.*, 2006).

Habitat loss to urbanisation and agricultural expansion reduces stopover site availability, which will eventually lead to higher densities of migrants using fewer sites (Wilcove &

Wikelski, 2008; Flockhart *et al.*, 2013, 2015; Chowdhury *et al.*, 2017). In general, high local densities and greater species diversity can lead to increases in both between– and within–species transmission of pathogens (Bradley & Altizer, 2005; Altizer, Bartel & Han, 2011; Satterfield, Maerz & Altizer, 2015).

Butterflies are sensitive to environmental factors, and slight changes can cause rapid population declines. Climate change is likely to affect moisture and temperature regimes, and thereby disrupt migratory cues. Anderson & Brower (1993) experimentally determined that surface water on the bodies of monarch butterflies at overwintering sites in Mexico affects their survival at low temperatures: 50% of dry butterflies were killed at –8 °C, and 100% at –14°C, but if their wings and bodies were wet, 50% died at –4°C, and 100% at –8°C. Larsen & Lee (1994) showed that wet monarchs freeze more rapidly than dry individuals and discussed the importance of intact oyamel fir forest to their survival. In addition, migrants are affected by wind patterns: stronger winds can carry the migrants far from their destination, and weak winds may increase the energy required to reach the destination (Cardé, 2008; Chapman *et al.*, 2008; Sydeman *et al.*, 2014).

Temperature and the availability of water resources can influence the abundance of migratory butterflies in various ways (Brower, Fink & Walford, 2006; Robinson *et al.*, 2009; Chowdhury *et al.*, 2021). Temperature and rainfall patterns are changing rapidly, and up to 69% of the overwintering area of the monarch butterfly could become unsuitable by 2030, with possibly none remaining suitable by the end of this century (Sáenz–Romero *et al.*, 2012; Ramírez *et al.*, 2015). Climate change is also associated with increased winter storms in Mexico, leading to substantial mortality of overwintering monarchs (Oberhauser & Peterson, 2003; Brower *et al.*, 2004; Berry *et al.*, 2005; Batalden *et al.*, 2014). Milkweeds are projected to shift northward in North America in both moderate (1–3°C increase) and severe (2–6°C increase) climate warming scenarios, with the potential for environmental cues for migration (e.g. photoperiod) becoming decoupled from the availability of food plants (Lemoine, 2015; Borkin, 2017).

The directional movement of migratory butterflies means they must cross linear features such as roads, and collisions with vehicles can cause substantial mortality (Kantola *et al.*, 2019; Tracy *et al.*, 2019). It has been estimated that 20 million butterflies including 500,000 monarchs are killed along roads in Illinois each week (McKenna *et al.*, 2001; Berenbaum, 2015). Kantola *et al*. (2019) estimated that nearly 2.1 million monarchs are killed annually in the Central Funnel in Texas, representing around 3% of the overwintering population. The presence of milkweed larval host plant (*Asclepias verticillata*) and other nectar resources (e.g. Asteraceae, *Trifolium* spp., and Apiaceae) along road verges means that roads attract butterflies, and measures such as speed–limiting vehicles at roadkill hotspots, especially during the peak migration period, could substantially reduce mortality (Kantola *et al.*, 2019). Obtaining credible data on the survival rates of butterflies during migration is difficult (Flockhart *et al.*, 2015), but such information will be essential for assessing the success of conservation interventions.

The causes of declines in migratory butterflies can be very difficult to diagnose. In the case of the monarch, much attention has focused on threats to their overwintering sites in Mexico (Brower *et al.*, 2002, 2012; Oberhauser & Peterson, 2003; Ramírez, Azcárate & Luna, 2003; Agrawal & Inamine, 2018), but as detailed above there are also substantial threats in their breeding range and during migration. It is likely that climate change (especially extreme events), and the distribution of host plants represent the most significant threats to migratory butterflies (Marini & Zalucki, 2017; Malcolm, 2018; Chowdhury *et al.*, 2020, 2021).

We have focused our discussion in this section on just one particularly well–studied migratory butterfly species, which is rather atypical in some ways: for example, its mixed strategy of migration to adult hibernation refugia is very unusual (perhaps unique) among migrant butterflies. By contrast, for the many species of 'more typical' butterfly migrants, there is a real lack of knowledge about population trends and conservation status. One of the few relatively well–studied species is the painted lady; this species carries out long–range migrations of approximately the same distance as monarchs (Stefanescu *et al.*, 2013), and also feeds on fast–growing weedy host plants of ephemeral habitats. However, in contrast to monarchs, painted ladies do not appear to be declining, at least in Europe (Fox *et al.*, 2015). A comparative study investigating similarities and differences between these two migrant species, and the impact of various life–history traits on their population trends would be instructive. Further work on the factors influencing decline in migratory butterflies, especially population–level studies, is urgently needed to assess connectivity between breeding and non–breeding grounds (Gao *et al.*, 2020) and population dynamics across the whole annual cycle.

## VIII. CONCLUSIONS

(1) Nearly 600 butterfly species are currently known to be migratory, and the rate at which new migrants are discovered shows no sign of slowing down (Fig. 4). Migratory butterflies occur all over the world except Antarctica, with most records from tropical countries with wet–dry seasonality (e.g. Australia, India, and Sri Lanka). However, the largest proportions of butterflies identified as migrants are from relatively well–studied regions of the world such as Europe, USA, and Australia, probably reflecting their greater interest in research on butterflies.

(2) We found 24 cases where a species was noted as sedentary by some authors, but was considered a migrant elsewhere in its range. This might reflect errors of course, but perhaps more likely suggests that such species have both migrant and non–migrant subgroups within the same population (partial migration; Menz *et al*., 2019). Using stable isotope analyses, Van der Zanden *et al*. (2018) recently found that 48% of monarchs from South Florida are migrants while the remainder are residents, lending support to the idea that partial migration might be common in butterflies.

(3) The proportion of migratory butterflies varied enormously taxonomically. Some 53% of Libytheinae butterflies are migratory, while the proportion is much lower in other subfamilies. Future studies should obtain regional records, document movement patterns, and conduct experimental work on migration in butterflies to reveal hotspots and their vulnerability to extinction, thus providing invaluable data for butterfly conservation. A fruitful avenue woul be to focus on mapping the distributions of migratory butterflies at different times of year.

(4) Many butterflies migrate from one part of the world to another every year. They cross international borders, and the biomass transfer during migratory flight is extensive (Hu *et al*., 2016). Despite this, we possess limited knowledge on their origin, stopover sites, and destination (Pierce *et al*., 2014). It took decades for scientists to establish the importance of studying butterfly migration and newer methods to investigate migratory patterns are now available. Although multiple methods to describe migratory behaviour exist, applications of most of these has been limited to just a few species (e.g. *D. plexippus*, *V. cardui*, *V. atalanta*). We remain far from understanding the true prevalence of migration in butterflies, and the existing evidence is rather weak for many species.

(5) About half of all lepidopteran species are estimated to be decreasing in abundance worldwide (Sánchez–Bayo & Wyckhuys, 2019; van Strien *et al.*, 2019; Van Klink *et al.*, 2020). If the acute declines recorded for the North American monarch are replicated in other migratory butterflies around the world, there might be hundreds of such declines that are going undetected. Successful conservation of migratory butterflies will depend on achieving a much better understanding of which species are migratory, and whether and why populations are declining.

## IX. ACKNOWLEDGEMENTS

We thank the Australian Government, the University of Queensland, and the Centre for Biodiversity and Conservation Science for providing an International Research Training Program Fellowship. We are grateful to Don R. Reynolds (Natural Resources Institute, University of Greenwich) for providing important feedback. We thank Stephen Malcolm (Department of Biological Sciences, Western Michigan University) for his comments, which greatly improved this review.

## X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Species determined to be migratory based on studies using a variety of different experimental, physiological or population evidence methods.

## XI. REFERENCES

References identified with an asterisk (*) were used in the literature review.

*ABBOTT, C. H. (1951). A quantitative study of the migration of the painted lady butterfly, *Vanessa cardui* L. *Ecology* **32**, 155–171.

*AGRAWAL, A. A. & INAMINE, H. (2018). Mechanisms behind the monarch's decline. *Science* **360**, 1294–1296.

*AGRAWAL, A. A. (2019). Advances in understanding the long–term population decline of monarch butterflies. *Proceedings of the National Academy of Sciences* **116**, 8093–8095.

*AITKEN, E. H. & E. COMBER. (1904). Butterflies of Konkan. *Journal of the Bombay Natural History Society* **15**, 42–55.

*AITKEN, E. H. (1886). A list of the butterflies of the Bombay Presidency in the society's collections. *Journal of the Bombay Natural History Society* **1**, 215–218.

*AITKEN, E. H. (1900). Butterflies as weather prophets. *Journal of the Bombay Natural History Society* **13**, 540–541.

*ÅKESSON, S. & HEDENSTRÖM, A. (2007). How migrants get there: migratory performance and orientation. *BioScience* **57**, 123–133.

*ALERSTAM, T., HEDENSTRÖM, A. & ÅKESSON, S. (2003). Long−distance migration: evolution and determinants. *Oikos* **103**, 247–260.

*ALTIZER, S. & DAVIS, A. K. (2010). Populations of monarch butterflies with different migratory behaviors show divergence in wing morphology. *Evolution: International Journal of Organic Evolution* **64**, 1018–1028.

*ALTIZER, S. M. (2001). Migratory behaviour and host–parasite co–evolution in natural populations of monarch butterflies infected with a protozoan parasite. *Evolutionary Ecology Research* **3**, 567–581.

*ALTIZER, S. M., OBERHAUSER, K. S. & BROWER, L. P. (2000). Associations between host migration and the prevalence of a protozoan parasite in natural populations of adult monarch butterflies. *Ecological Entomology* **25**, 125–139.

*ALTIZER, S. M., BARTEL, R. & HAN, B. A. (2011). Animal migration and infectious disease risk. *Science* **331**, 296–302.

*ALTIZER, S., HOBSON, K. A., DAVIS, A. K., DE ROODE, J. C. & WASSENAAR, L. I. (2015). Do healthy monarchs migrate farther? Tracking natal origins of parasitized vs. uninfected monarch butterflies overwintering in Mexico. *PloS One* **10**, e0141371.

*ANDERSON, J. B. & BROWER, L. P. (1993). Cold–hardiness in the annual cycle of the monarch butterfly. In *Biology and conservation of the monarch butterfly* (eds S. B. Malcolm & M. P. Zalucki), Natural History Museum of Los Angeles County, Los Angeles, CA, pp. 157–164.

*ANDERSON, R. C. (2009). Do dragonflies migrate across the western Indian Ocean?. *Journal of tropical Ecology* **25**, 347–358.

*ANTRAM, C. B. (1924). *Butterflies of India*. Mittal Publications, 226 pp.

*ARALIMARAD, P., REYNOLDS, A. M., LIM, K. S., REYNOLDS, D. R. & CHAPMAN, J. W. (2011). Flight altitude selection increases orientation performance in high–flying nocturnal insect migrants. *Animal Behaviour* **82**, 1221–1225.

*ARBOGAST, R. T. (1966). Migration of *Agraulis vanillae* (Lepidoptera, Nymphalidae) in Florida. *The Florida Entomologist* **49**, 141–145.

*ARCHIBALD, S. B., BOSSERT, W. H., GREENWOOD, D. R. & FARRELL, B. D. (2010). Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* **36**, 374–398.

*AUSTIN, G. T. (1992). *Cercyonis pegala* (Fabricius)(Nymphalidae: Satyrinae) in the Great Basin: new subspecies and biogeography. *Bulletin of the Allyn Museum (USA)* **135**, 1–60.

*AUSTIN, G. T. (1997). The Butterflies of Venezuela. Part 1: Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae). A Comprehensive Guide to the Identification of Adult Nymphalidae, Papilionidae, and Pieridae. *Journal of the New York Entomological Society* **104**, 236–239.

*AUSTIN, G. T., MILLER, L. D. & MILLER, J. Y. (2007). Taxonomic Comments on *Pseudolycaena wallengren* (Lepidoptera: Lycaenidae: Theclinae: Eumaeini). *Bulletin of the Allyn Museum* **149**, 1–22.

*BACHELOR, D. M. (1960). A large scale migration of *Euploea modesta* Butler. *Malayan Nature Journal* **14**, 90–94.

*BAGUETTE, M. (2003). Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography* **26**, 153–160.

*BAGUETTE, M., PETIT, S. & QUÉVA, F. (2000). Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology* **37**, 100–108.

*BAGUETTE, M., VANSTEENWEGEN, C., CONVI, I. & NEVE, G. (1998). Sex–biased density–dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. *Acta Oecologica* **19**, 17–24.

*BAJER, F. J. (1999). The fall migration of the monarch butterflies–Comment. *American Neptune* **59**, 75–76.

*BAKER, R. R. (1969). The evolution of the migratory habit in butterflies. *The Journal of Animal Ecology* **28**, 703–746.

*BALCIUNAS, J. & KNOPF, K. (1977). Orientation, flight speeds, and tracks of three species of migrating butterflies. *Florida Entomologist* **60**, 37–39.

*BALL, E. D. & STONE, W. E. (1928). A Puzzling Butterfly Migration. *Science* **68**, 110–111.

*BARCANT, M. (1971). *Butterflies of Trinidad and Tobago*. Collins, 314 pp.

*BARTEL, R. A., OBERHAUSER, K. S., DE ROODE, J. C. & ALTIZER, S. M. (2011). Monarch butterfly migration and parasite transmission in eastern North America. *Ecology* **92**, 342–351.

*BASSET, Y. (2001). Invertebrates in the canopy of tropical rain forests How much do we really know?. *Plant Ecology* **153**, 87–107.

*BASSET, Y., BARRIOS, H., SEGAR, S., SRYGLEY, R. B., AIELLO, A., WARREN, A. D., DELGADO, F., CORONADO, J., LEZCANO, J., ARIZALA, S. & RIVERA, M. (2015). The butterflies of Barro Colorado Island, Panama: local extinction since the 1930s. *PLoS One* **10**, e0136623.

*BATALDEN, R. V., OBERHAUSER, K. & PETERSON, A. T. (2014). Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. *Environmental Entomology* **36**, 1365–1373.

*BECCALONI, G. W. (1997). Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Tropical Lepidoptera Research* **8**, 103–124.

*BECKER, V. O. & MILLER, S. E. (1992). The butterflies of Guana Island, British Virgin Islands. *Bulletin of the Allyn Museum (USA)* **136**, 1–10.

*BEEBE, W. (1950*a*). Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae (butterflies) at Rancho Grande, north–central Venezuela. *Zoologica* **35**, 57–68.

*BEEBE, W. (1950*b*). Migration of Pieridae (butterflies) through Portachuelo Pass, Rancho Grande, north–central Venezuela. *Zoologica* **35**, 189–196.

*BEEBE, W. M. (1923). Notes on Galapagos lepidoptera. *Zoologica*, **5**, 51–59.

*BEEBE, W. M. (1949a). Insect migration at Rancho Grande in north–central Venezuela. *Zoologica* **34**, 107–110.

*BEEBE, W. M. (1949b). Migration of Papilionidae at Rancho Grande, north–central Venezuela. *Zoologica* **34**, 119–126.

*BEEBE, W. M. (1951). Migration of Nymphalidae (Nymphalinae), Brassolidae, Morphidae, Libytheidae, Satyridae, Riodinidae, Lycaenidae and Hesperiidae (Butterflies) through Portachuelo Pass, Rancho Grande, north–central Venezuela. *Zoologica* **36**, 1–16.

*BELL, T. R. (1910). The common butterflies of the plains of India. *Journal of the Bombay Natural History Society* **20**, 279–330.

*BELL, T. R. (1912). The common butterflies of the plains of India (including those met with in the hill stations of the Bombay presidency). Part XII. Family Pieridae. *Journal of the Bombay Natural History Society* **21**, 1131–1157.

*BELTH, J. E. (2012). *Butterflies of Indiana: a field guide*. Indiana University Press, 344 pp.

BENSCH, S. & ÅKESSON, M. (2005). Ten years of AFLP in ecology and evolution: why so few animals? *Molecular Ecology* **14**, 2899–2914.

BENSCH, S., ÅKESSON, S. & IRWIN, D. E. (2002). The use of AFLP to find an informative SNP: genetic differences across a migratory divide in willow warblers. *Molecular Ecology* **11**, 2359–2366.

*BENSUSAN, K. J., NESBIT, R., PEREZ, C. E., TRYJANOWSKI, P. & ZDUNIAK, P. (2014). Species composition and dynamics in abundance of migrant and sedentary butterflies

(Lepidoptera) at Gibraltar during the spring period. *European Journal of Entomology* **111**, 555–559.

*BENVENUTI, S., ANTONIA, P. D. & IOALÈ, P. (1994). Migration pattern of the red admiral, *Vanessa atalanta* L.(Lepidoptera, Nymphalidae), in Italy. *Italian Journal of Zoology* **61**, 343–351.

*BENVENUTI, S., DALL'ANTONIA, P. & IOALÈ, P. (1996). Directional preferences in the autumn migration of the red admiral (*Vanessa atalanta*). *Ethology* **102**, 177–186.

*BERDYUGINA, S. V. & HENRY, G. W. (2007). Butterfly diagram and activity cycles in HR 1099. *The Astrophysical Journal Letters* **659**, L157–L160.

*BERENBAUM, M. (2015). Road worrier. *American Entomologist* **61**, 5–8.

*BERGMAN, K. O. & LANDIN, J. (2001). Distribution of occupied and vacant sites and migration of Lopinga achine (Nymphalidae: Satyrinae) in a fragmented landscape. *Biological Conservation* **102**, 183–190.

*BERRY, P., HARRISON, P., DAWSON, T. & WALMSLEY, C. (2005). Modelling natural resource responses to climate change (MONARCH): a local approach. In *Development of a conceptual and methodological framework for universal application*. Environmental Change Institute, University of Oxford, 270 pp.

*BERTHOLD, P. (1999). A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* **70**, 1–11.

*BESHKOV, S. (1996*a*). Migrant Lepidoptera species in Albania and Macedonia in 1995. *Atalanta* **27**, 535–543.

*BESHKOV, S. (1996*b*). Migrant Lepidoptera species in Bulgaria in 1995. *Atalanta* **27**, 517–533.

*BHAROS, A. M. K. (2000). Large scale emergence and migration of the common emigrant butterflies *Catopsilia pomona* (Family: Pieridae). *Journal of the Bombay Natural History Society* **97**, 301–301.

*BHAUMIK, V. & KUNTE, K. (2018). Female butterflies modulate investment in reproduction and flight in response to monsoon−driven migrations. *Oikos* **127**, 285–296.

*BOLOTOV, I., PODBOLOTSKAYA, M., KOLOSOVA, Y. S. & ZUBRII, N. (2013). The current flow of migrants and its contribution to butterfly faunas (Lepidoptera, Rhopalocera) on marine islands with young allochthonous biota. *Biology Bulletin* **40**, 78–88.

*BORGHESIO, L. & WAGURA, L. The Common Butterflies of the Mathews Range.

*BORKIN, S. S. (2017). Notes on shifting distribution patterns and survival of immature *Danaus plexippus* (Lepidoptera: Danaidae) on the food plant *Asclepias syriaca*. *The Great Lakes Entomologist* **15**, 199–206.

*BOWLIN, M. S., BISSON, I. A., SHAMOUN–BARANES, J., REICHARD, J. D., SAPIR, N., MARRA, P. P., KUNZ, T. H., WILCOVE, D. S., HEDENSTRÖM, A., GUGLIELMO, C. G., ÅKESSON, S. & WIKELSKI, M. (2010). Grand challenges in migration biology. *Integrative and Comparative Biology* **50**, 261–279.

*BRABY, M. F. (2016a). *The complete field guide to butterflies of Australia*. CSIRO Publishing, 400 pp.

*BRABY, M. F. (2016b). Migration records of butterflies (Lepidoptera: Papilionidae, Hesperiidae, Pieridae, Nymphalidae) in the 'Top End' of the Northern Territory. *The Australian Entomologist* **43**, 151–160.

*BRABY, M. F. & EDWARDS, T. D. (2006). The butterfly fauna of the Griffith district, a fragmented semi–arid landscape in inland southern New South Wales. *Pacific Conservation Biology* **12**, 140–154.

*BRABY, M. F. (2005a). *Complete Field Guide to Butterflies of Australia*. CSIRO publishing, 339 pp.

*BRABY, M. F. (2005b). Migration of two species of Pieridae (Lepidoptera: Papilionoidea) in southeastern Australia. *The Australian Entomologist* **32**, 83–92.

*BRABY, M. F. (2000). *Butterflies of Australia: their identification, biology and distribution*. Collingwood: CSIRO publishing, 976 pp.

*BRABY, M. F. (1991). Migration of' *Euploea core corinna* (WS Macleay) (Nymphalidae: Danainae) in northern Queensland, Australia. *The Australian Entomologist* **18**, 143–146.

*BRABY, M. F. (1988). A note on directional flights of '*Eurema smilax*' (Donovan) (Lepidoptera: Pieridae) and '*Danaus chrysippus petilia*' (Stoll) (Lepidoptera: Nymphalidae) in Victoria. *The Australian Entomologist* **15**, 53–57.

BRADLEY, C. A. & ALTIZER, S. (2005). Parasites hinder monarch butterfly flight: implications for disease spread in migratory hosts. *Ecology Letters* **8**, 290–300.

*BRATTSTRÖM, O., ÅKESSON, S. & BENSCH, S. (2010*a*). AFLP reveals cryptic population structure in migratory European red admirals (*Vanessa atalanta*). *Ecological Entomology* **35**, 248–252.

*BRATTSTRÖM, O., BENSCH, S., WASSENAAR, L. I., HOBSON, K. A. & ÅKESSON, S. (2010*b*). Understanding the migration ecology of European red admirals *Vanessa atalanta* using stable hydrogen isotopes. *Ecography* **33**, 720–729.

*BRATTSTRÖM, O., KJELLÉN, N., ALERSTAM, T. & ÅKESSON, S. (2008). Effects of wind and weather on red admiral, *Vanessa atalanta*, migration at a coastal site in southern Sweden. *Animal Behaviour* **76**, 335–344.

*BRATTSTRÖM, O. (2007). *Ecology of red admiral migration*. Lund University, 136 pp.

*Brindza, L. J., Brower, L. P., Davis, A. K. & Van Hook, T. (2008). Comparative success of monarch butterfly migration to overwintering sites in Mexico from inland and coastal sites in Virginia. *Journal of the Lepidopterists' Society* **62**, 189–200.

*Brodsky, A. K. (1991). Vortex formation in the tethered flight of the peacock butterfly Inachis io L.(Lepidoptera, Nymphalidae) and some aspects of insect flight evolution. *Journal of Experimental Biology* **161**, 77–95.

*Broekhuysen, J. G. P. (1960). Butterfly migration over Johannesburg. *South African Journal of Science* **56**, 237–239.

*Brower, L. P., Fink, L. S., Kiphart, R. J., Pocius, V., Zubieta, R. R. & Ramírez, M. I. (2015). Effect of the 2010–2011 drought on the lipid content of monarchs migrating through Texas to overwintering sites in Mexico. In *Monarchs in a Changing World: Biology and Conservation of an Iconic Butterfly* (eds K. S. Oberhauser, K. R. Nail & S. Altizer), Cornell University Press, pp. 117–129.

*Brower, L. P., Taylor, O. R., Williams, E. H., Slayback, D. A., Zubieta, R. R. & Ramirez, M. I. (2012). Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity* **5**, 95–100.

*Brower, L. P., Fink, L. S. & Walford, P. (2006). Fueling the fall migration of the monarch butterfly. *Integrative and Comparative Biology* **46**, 1123–1142.

*Brower, L. P., Kust, D. R., Rendon–Salinas, E., Serrano, E. G., Kust, K. R., Miller, J., Fernandez del Rey, C. & Pape, K. (2004). Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. In *The monarch butterfly: biology and conservation* (eds K. S. Oberhauser & M. J. Solensky), Cornell University Press, pp. 151–166.

*BROWER, L. P., CASTILLEJA, G., PERALTA, A., LOPEZ−GARCIA, J., BOJORQUEZ−TAPIA, L., DÍAZ, S., MELGAREJO, D. & MISSRIE, M. (2002). Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. *Conservation Biology* **16**, 346–359.

*BROWER, L. P. (1996). Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology* **199**, 93–103.

*BROWER, L. P. (1995). Understanding and misunderstanding the migration of the monarch butterfly(Nymphalidae) in North America: 1857–1995. *The Journal of the Lepidopterists' Society* **49**, 304–385.

*BROWER, L. P. & MALCOLM, S. B. (1991). Animal migrations: endangered phenomena. *American Zoologist* **31**, 265–276.

*BROWER, L. P. (1977). Monarch migration. *Natural History* **86**, 40–53.

*BROWER, L. P. (1961). Studies on the migration of the monarch butterfly I. Breeding populations of *Danaus plexippus* and *D. gilippus berenice* in south central Florida. *Ecology* **42**, 76–83.

*BROWN, I. L. & EHRLICH, P. R. (1980). Population biology of the checkerspot butterfly, Euphydryas chalcedona structure of the Jasper Ridge colony. *Oecologia* **47**, 239–251.

*BROWN, K. (2001). Animal magnetism guides migration, *Science* **294**, 283–284.

BUCHER, E. H. (1992). The causes of extinction of the passenger pigeon. In *Current Ornithology* (eds D. M. Power), Springer, Boston, MA, pp. 1–36.

*BURWELL, C. J., MCDOUGALL, A., NAKAMURA, A. & LAMBKIN, C. L. (2011). New butterfly, hawkmoth (Lepidoptera) and dragonfly (Odonata) records from vegetated coral cays in the southern Great Barrier Reef, Queensland. *The Australian Entomologist* **38,** 75–88.

*CALVERT, W. H., HEDRICK, L. E. & BROWER, L. P. (1979). Mortality of the monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. *Science* **204**, 847–851.

*CAMPBELL, D. L. & PIERCE, N. E. (2003). Phylogenetic relationships of the Riodinidae: implications for the evolution of ant association. In *Butterflies: Ecology and Evolution Taking Flight* (eds C. L. Boggs, W. B. Watt & P. R. Ehrlich), Chicago University Press, pp. 395–408.

*CANT, E. T., SMITH, A. D., REYNOLDS, D. R. & OSBORNE, J. L. (2005). Tracking butterfly flight paths across the landscape with harmonic radar. *Proceedings of the Royal Society B: Biological Sciences* **272**, 785–790.

*CARDÉ, R. T. (2008). Insect migration: do migrant moths know where they are heading? *Current Biology* **18**, R472–R474.

*CARDON, R. (1927). On a migration of *Catopsilia pomona* (F.). *Journal of the Malayan Branch of the Royal Asiatic Society* **5**, 314–315.

*CHAN, C.–H. (2004). *Hong Kong butterfly conservation*. The University of Hong Kong, 117 pp.

*CHANG, H. S. (2012). A catalogue of the butterflies of China. University of California Libraries, 228 pp.

*CHAO, R. F., CHEN, T. Y. & YANG, P. S. (2008). Influences of temperature and photoperiod on the breakup and spring remigration of overwintering aggregations of *Euploea* spp. and *Tirumala septentrionis* in Dawu, Southeastern Taiwan. *The Pan–Pacific Entomologist* **84**, 254–256.

*CHAPMAN, B. B., BRÖNMARK, C., NILSSON, J. Å. & HANSSON, L. A. (2011). The ecology and evolution of partial migration. *Oikos* **120**, 1764–1775.

*CHAPMAN, J. W. & DRAKE, V. A. (2016). Insect migration. In *Encyclopedia of Animal Behavior* (eds M. D. Breed & J. Moore), Cambridge University Press, pp. 161–166.

*CHAPMAN, J. W., REYNOLDS, D. R. & WILSON, K. (2015). Long–range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecology Letters* **18**, 287–302.

*CHAPMAN, J. W., BELL, J. R., BURGIN, L. E., REYNOLDS, D. R., PETTERSSON, L. B., HILL, J. K., BONSALL, M. B. & THOMAS, J. A. (2012). Seasonal migration to high latitudes results in major reproductive benefits in an insect. *Proceedings of the National Academy of Sciences* **109**, 14924–14929.

*CHAPMAN, J. W., DRAKE, V. A. & REYNOLDS, D. R. (2011). Recent insights from radar studies of insect flight. *Annual Review of Entomology* **56**, 337–356.

*CHAPMAN, J. W., NESBIT, R. L., BURGIN, L. E., REYNOLDS, D. R., SMITH, A. D., MIDDLETON, D. R. & HILL, J. K. (2010). Flight orientation behaviors promote optimal migration trajectories in high–flying insects. *Science* **327**, 682–685.

*CHAPMAN, J. W., REYNOLDS, D. R., HILL, J. K., SIVELL, D., SMITH, A. D. & WOIWOD, I. P. (2008). A seasonal switch in compass orientation in a high–flying migrant moth. *Current Biology* **18**, R908–R909.

*CHARRETTE, N. A., CLEARY, D. F. R. & MOOERS, A. Ø. (2006). Range−restricted, specialist Bornean butterflies are less likely to recover from ENSO−induced disturbance. *Ecology* **87**, 2330–2337.

*CHATURVEDI, N. (1992). Northward migration of the Common Indian Crow butterfly *Euploea core* (Cramer) in and around Bombay. *Journal of the Bombay Natural History Society* **90**, 115–116.

*CHECA, M. F., RODRIGUEZ, J., WILLMOTT, K. R. & LIGER, B. (2014). Microclimate variability significantly affects the composition, abundance and phenology of butterfly communities in a highly threatened neotropical dry forest. *Florida Entomologist* **97**, 1–13.

*CHOWDHURY, S. H. & HOSSAIN, M. (2013). *Butterflies of Bangladesh: A Pictorial Handbook*. Skylark Printers, 260 pp.

CHOWDHURY, S, BRABY, M. F., FULLER, R. A. & ZALUCKI, M. P. (2021a). Coasting along to a wider range: niche conservatism in the recent range expansion of the Tawny Coster, Acraea terpsicore (Lepidoptera: Nymphalidae). *Diversity and Distributions* **27**, 412–415.

CHOWDHURY, S., ALAM, S., CHOWDHURY, S. U., ROKONUZZAMAN, M., SHAHRIAR, S. A., SHOME, A. R. & FULLER, R. A. (2021b). Butterflies are weakly protected in a mega–populated country, Bangladesh. *Global Ecology and Conservation* **26**, e01484.

CHOWDHURY, S., HESSELBERG, T., BÖHM, M., ISLAM, M. R. & AICH, U. (2017). Butterfly diversity in a tropical urban habitat (Lepidoptera: Papilionoidea). *Oriental Insects* **51**, 417–430.

*CHU, J. R. (2011). Butterflies: A Continuing Study of Species and Populations in Boulder County Open Space Properties –2011 Inventory and 2007–2011 Analyses. C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Ft. Collins, CO, 95 pp.

*CHU, J. (2010). *Butterfly Inventories in Boulder County Open Space Properties*. Unpublished report for Boulder County Parks and Open Space, Boulder, CO, 42 pp.

*CHU, J. (2009). *Inventories of Butterflies in Boulder County*. Unpublished report for Boulder County Parks and Open Space, Boulder, C*O*, 39 pp.

*CHU, J. P. & SPORTIELLO, M. (2007). *Butterfly research in Boulder County, Colorado 2004–2007*, Colorado State University, 86 pp.

*CIOC, M. (2009). *The game of conservation: international treaties to protect the world's migratory animals* (illustrated ed.): Ohio University Press, 232 pp.

*CIZEK, O. & KONVICKA, M. (2005). What is a patch in a dynamic metapopulation? Mobility of an endangered woodland butterfly, *Euphydryas maturna*. *Ecography* **28**, 791–800.

*CLARK, A. H. (1931). Some observations on butterfly migrations. *The Scientific Monthly* **32**, 150–155.

*CLARKE, A. R. & ZALUCKI, M. P. (2004). Monarchs in Australia: on the winds of a storm?. *Biological Invasions* **6**, 123–127.

*CLEMENTS, J. C. (2012). First record of the Fiery Skipper, *Hylephila phyleus* Drury (Lepidoptera: Hesperiidae) from New Brunswick, Canada. *Journal of the Acadian Entomological Society* **8**, 59–60.

*CLENCH, H. K. (1968). Butterflies from Coahuila, Mexico. *Journal of the Lepidopterists' Society* **22**, 227–231.

COHEN, E. B., RUSHING, C. R., MOORE, F. R., HALLWORTH, M. T., HOSTETLER, J. A., RAMIREZ, M. G. & MARRA, P. P. (2019). The strength of migratory connectivity for birds en route to breeding through the Gulf of Mexico. *Ecography* **42**, 658–669.

*CONNAHS, H., RHEN, T. & SIMMONS, R. B. (2016). Physiological perturbation reveals modularity of eyespot development in the painted lady butterfly, *Vanessa cardui*. *PloS One*, **11**, e0161745.

*COOK, L. M., DENNIS, R. L. & HARDY, P. B. (2001). Butterfly−hostplant fidelity, vagrancy and measuring mobility from distribution maps. *Ecography* **24**, 497–504.

CRESSWELL, J. E. (2011). A meta–analysis of experiments testing the effects of a neonicotinoid insecticide (imidacloprid) on honey bees. *Ecotoxicology* **20**, 149–157.

*CREWE, T. L. & MCCRACKEN, J. D. (2015). Long–term trends in the number of monarch butterflies (Lepidoptera: Nymphalidae) counted on fall migration at Long Point, Ontario, Canada (1995–2014). *Annals of the Entomological Society of America* **108**, 707–717.

*CRYAN, P. M., BOGAN, M. A., RYE, R. O., LANDIS, G. P. & KESTER, C. L. (2004). Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long–distance migration. *Journal of Mammalogy* **85**, 995–1001.

*CULOTTA, E. (1992). The case of the missing monarchs. *Science* **256**, 1275–1276.

*D'ABRERA, B. (1985). *Butterflies of the Oriental Region. Part II. Nymphalidae, Satyridae and Amathusidae,* Hill House publishers, pp. 246–534.

*D'ABRERA, B. (1984). *Butterflies of the Neotropical Region. Part II. Danaidae, Ithomiidae, Heliconidae and Morphidae*. Hill House publishers, 222 pp.

*DANTHANARAYANA, W. (2012). *Insect flight: dispersal and migration*. Springer Science & Business Media, 289 pp.

*DARWIN, C. (1903). *More letters of Charles Darwin.* D, (eds F. Darwin & A. C. Seward, Appleton and Company, New York, 515 pp.

*DAVID, G. (1982). The butterflies of Kent Island, Grand Manan, New Brunswick. *Journal of the Lepidopterists' Society* **36**, 264–268.

*DAVIDSON, J., BELL, T. R. & AITKEN, E. H. (1896). The butterflies of the North Canara district of the Bombay Presidency. Part I. *Journal of the Bombay Natural History Society* **10**, 237–259.

*Davis, A. K. (2015). Opinion: conservation of monarch butterflies (*Danaus plexippus*) could be enhanced with analyses and publication of citizen science tagging data. *Insect Conservation and Diversity* **8**, 103–106.

*Davis, A. K. (2012). Are migratory monarchs really declining in eastern North America? Examining evidence from two fall census programs. *Insect Conservation and Diversity* **5**, 101–105.

*Davis, A. K. & Rendón–Salinas, E. (2010). Are female monarch butterflies declining in eastern North America? Evidence of a 30–year change in sex ratios at Mexican overwintering sites. *Biology Letters* **6**, 45–47.

*Davis, A. K. & Garland, M. S. (2002). An evaluation of three methods of counting migrating monarch butterflies in varying wind conditions. *Southeastern Naturalist* **1**, 55–68.

*Dawson, T. P., Berry, P. M., Harrison, P. A. & Pearson, R. G. (2004). Modelling long–distance seed dispersal across fragmented landscapes. In *Landscape ecology of trees and forests. Proceedings of the twelfth annual IALE (UK) conference, Cirencester, UK*. International Association for Landscape Ecology (IALE (UK)), pp. 43–49.

*de la Torre y Callejas, S. L. (1954). An annotated list of the butterflies and skippers of Cuba (Lepidoptera, Rhopalocera). *Journal of the New York Entomological Society* **62**, 1–25.

*De Rhe–Philipe, G. W. V. (1902). The butterflies of the Lucknow district. *Journal of the Bombay Natural History Society* **14**, 481–493.

*de Roode, J. C., Pedersen, A. B., Hunter, M. D. & Altizer, S. (2008). Host plant species affects virulence in monarch butterfly parasites. *Journal of Animal Ecology* **77**, 120–126.

*DELL, B. (1977). Migration of' *Papilio demoleus sthenelus*' WS Macleay (Lepidoptera: Papilionidae) in Western Australia. *The Australian Entomologist* **3**, 83–86.

*DENNIS, R. L., SHREEVE, T. G. & SPARKS, T. H. (1998). The effects of island area, isolation and source population size on the presence of the grayling butterfly *Hipparchia semele* (L.) (Lepidoptera: Satyrinae) on British and Irish offshore islands. *Biodiversity and Conservation* **7**, 765–776.

DENNO, R. F. & GRISSELL, E. E. (1979). The adaptiveness of wing−dimorphism in the salt marsh−inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* **60**, 221–236.

DENNO, R. F., DOUGLAS, L. W. & JACOBS, D. (1985). Crowding and host plant nutrition: environmental determinants of wing−form in *Prokelisia marginata*. *Ecology* **66**, 1588–1596.

DENNO, R. F., RAUPP, M. J., TALLAMY, D. W. & REICHELDERFER, C. F. (1980). Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* **61**, 859–867.

*DE VRIES, P. J. (1987). *The butterflies of Costa Rica and their natural history*, Princeton University Press, 327 pp.

*DE VRIES, P., CHACON, I. & MURRAY, D. (1992). Toward a better understanding of host use and biodiversity in riodinid butterflies(Lepidoptera). *Journal of Research on the Lepidoptera* **31**, 103–126.

DHANJAL−ADAMS, K. L., KLAASSEN, M., NICOL, S., POSSINGHAM, H. P., CHADÈS, I. & FULLER, R. A. (2017). Setting conservation priorities for migratory networks under uncertainty. *Conservation Biology* **31**, 646–656.

*DINCĂ, V., CUVELIER, S., SZÉKELY, L. & VILA, R. (2009). New data on the Rhopalocera (Lepidoptera) of Dobrogea (south–eastern Romania). *Phegea* **37**, 1–21.

*DINGLE, H. (2014). *Migration: the biology of life on the move,* Oxford University Press; 2nd edition, 352 pp.

*DINGLE, H. (2009). Migration. In *Encyclopedia of Insects (Second Edition),* Elsevier, pp. 628–633.

*DINGLE, H. & DRAKE, V. A. (2007). What is migration? *Bioscience* **57**, 113–121.

*DINGLE, H. (2006). Animal migration: is there a common migratory syndrome? *Journal of Ornithology* **147**, 212–220.

*DINGLE, H., ZALUCKI, M., ROCHESTER, W. & ARMIJO–PREWITT, T. (2005). Distribution of the monarch butterfly, *Danaus plexippus* (L.) (Lepidoptera: Nymphalidae), in western North America. *Biological Journal of the Linnean Society* **85**, 491–500.

*DINGLE, H. (2001). The evolution of migratory syndromes in insects. In *Insect movement: mechanisms and consequences* (eds I. Woiwood, D. R. Reynolds & C. D. Thomas), Proceedings of the Royal Entomological Society's 20th Symposium, pp. 159–181.

*DINGLE, H., ROCHESTER, W. A. & ZALUCKI, M. P. (2000). Relationships among climate, latitude and migration: Australian butterflies are not temperate–zone birds. *Oecologia* **124**, 196–207.

*DINGLE, H., ZALUCKI, M. P. & ROCHESTER, W. A. (1999). Season−specific directional movement in migratory Australian butterflies. *Austral Entomology* **38**, 323–329.

*DINGLE, H. & WINCHELL, R. (1997). Juvenile hormone as a mediator of plasticity in insect life histories. *Archives of Insect Biochemistry and Physiology: Published in Collaboration with the Entomological Society of America* **35**, 359–373.

*DINGLE, H. (1996). *Migration : the biology of life on the move*. New York ; Oxford: Oxford University Press, 480 pp.

*DINGLE H. (1978) Migration and Diapause in Tropical, Temperate, and Island Milkweed Bugs, In *Evolution of Insect Migration and Diapause,* (ed H. Dingle). Proceedings in Life Sciences. Springer, New York, NY, 286 pp.

*DINGLE, H. (1972). Migration strategies of insects. *Science* **175**, 1327–1335.

*DIXON, C. A., ERICKSON, J. M., KELLETT, D. N. & ROTHSCHILD, M. (1978). Some adaptations between *Danaus plexippus* and its food plant, with notes on *Danaus chrysippus* and *Euploea core* (Insecta: Lepidoptera). *Journal of Zoology* **185**, 437–467.

*DOCKX, C., BROWER, L. P., WASSENAAR, L. I. & HOBSON, K. A. (2004). Do North American monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. *Ecological Applications* **14**, 1106–1114.

*DOUGLAS, M. M. & GRULA, J. W. (1978). Thermoregulatory adaptations allowing ecological range expansion by the pierid butterfly, *Nathalis iole* Boisduval. *Evolution* **32**, 776–783.

*DRAKE, V. A. & GATEHOUSE, A. G. (1995). *Insect migration: tracking resources through space and time*, Cambridge University Press, 500 pp.

*DRAKE, V. & FARROW, R. (1988). The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology* **33**, 183–210.

*DRAKE, V. & FARROW, R. (1985). A radar and aerial−trapping study of an early spring migration of moths (Lepidoptera) in inland New South Wales. *Austral Ecology* **10**, 223–223.

*DUCATEZ, S. & BAGUETTE, M. (2016). Inter−individual variation in shivering behaviour in the migratory painted lady *Vanessa cardui*. *Ecological Entomology* **41**, 131–137.

*DUDGEON, G. C. (1902). The migration of butterflies in the Kangra Valley. *Journal of the Bombay Natural History Society* **14**: 147–148.

*DUDLEY, R. & SRYGLEY, R. B. (2008). Airspeed adjustment and lipid reserves in migratory Neotropical butterflies. *Functional Ecology* **22**, 264–270.

*DUNN, K. L. (2020). Notes on migrations of the Brown Awl, *Badamia exclamationis* (Fabricius, 1775) (Lepidoptera: Hesperiidae) in north–eastern Queensland. *Calodema* **830**, 1–13.

*DUNN, K. L. & PETRIE, E. (2017). Arrival of the Tawny Coster butterfly in the Bowen region, Queensland. *Victorian Entomologist* **47**, 109–112.

*DUNN, K. L. & DUNN, L. E. (1991). *Review of Australian butterflies: distribution, Life history and Taxonomy. Parts 1–4*. Published by authors: Melbourne, 660 pp.

*DYER, L. A. & FORISTER, M. L. (2016). Wherefore and whither the modeler: understanding the population dynamics of monarchs will require integrative and quantitative techniques. *Annals of the Entomological Society of America* **109**, 172–175.

*EANES, W. F. & KOEHN, R. K. (1978). An analysis of genetic structure in the monarch butterfly, *Danaus plexippus* L. *Evolution* **32**, 784–797.

*EARLY, J. W., PARRISH, G. R. & RYAN, P. A. (1995). An invasion of Australian blue moon and blue tiger butterflies (Lepidoptera: Nymphalidae) in New Zealand. *Records of the Auckland Institute and Museum* **32**, 45–53.

*EHRLICH, P. R. & GILBERT, L. E. (1973). Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. *Biotropica* **5**, 69–82.

*EHRLICH, P. R. (1986). Which animal will invade?. In *Ecology of biological invasions of North America and Hawaii* (eds H. A. Mooney & J. A. Drake), Springer, pp. 79–95.

ESPELAND, M., HALL, J. P., DEVRIES, P. J., LEES, D. C., CORNWALL, M., HSU, Y.–F., WU, L.–W., CAMPBELL, D. L., TALAVERA, G. & VILA, R. (2015). Ancient Neotropical origin and recent recolonisation: Phylogeny, biogeography and diversification of the Riodinidae (Lepidoptera: Papilionoidea). *Molecular Phylogenetics and Evolution* **93**, 296–306.

*ESPESET, A. E., HARRISON, J. G., SHAPIRO, A. M., NICE, C. C., THORNE, J. H., WAETJEN, D. P., FORDYCE, J. A. & FORISTER, M. L. (2016). Understanding a migratory species in a changing world: climatic effects and demographic declines in the western monarch revealed by four decades of intensive monitoring. *Oecologia* **181**, 819–830.

*EVANS, W. H. (1910). A list of the butterflies of the palni hills with the descriptions of two new species, *Journal of the Bombay Natural History Society* **20,** 380–391.

*EVERSHED, J. (1912). Butterfly Migration in Relation to Mimicry. *Nature* **89**, 659–659.

*EVERSHED, J. (1910). Note on migration. *Journal of the Bombay Natural History Society* **20**, 390–391.

*FENTON, C. L. (1919). Insect Migration in Floyd and Adjoining Counties of Iowa. *American Midland Naturalist* **6**, 13–15.

*FERNALD, H. T. (1937). An unusual type of butterfly migration. *The Florida Entomologist*, **19**, 55–57.

*FERRIS, C. D. (1993). Reassessment of the *Colias alexandra* group, the Legume–feeding species, and preliminary cladistic analysis of the North American *Colias* (Pieridae: Coliadinae). *Bulletin of the Allyn Museum* **138**, 1–92.

*FERRIS, C. D. (1989). A new species of *Colias* from Utah (Pieridae: Coliadinae). *Bulletin of the Allyn Museum* **128**, 1–12.

*FERRIS, C. D. (1988). Revision of several North American Leguminosae feeding *Colias* species, with description of a new subspecies (Pieridae: Coliadinae). *Bulletin of the Allyn Museum* **116**, 1–28.

*FISHER, K. (1945). Four butterfly migrations in India and Ceylon. *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* **20**, 77–81.

*FLEISHMAN, E., MURPHY, D. D. & AUSTIN, G. T. (1999). Butterflies of the Toquima Range, Nevada: distribution, natural history, and comparison to the Toiyabe Range. *The Great Basin Naturalist* **59**, 50–62.

*FLOCKHART, D. T., BROWER, L. P., RAMIREZ, M. I., HOBSON, K. A., WASSENAAR, L. I., ALTIZER, S. & NORRIS, D. R. (2017a). Regional climate on the breeding grounds predicts variation in the natal origin of monarch butterflies overwintering in Mexico over 38 years. *Global Change Biology* **23**, 2565–2576.

*FLOCKHART, D. T., FITZ–GERALD, B., BROWER, L. P., DERBYSHIRE, R., ALTIZER, S., HOBSON, K. A., WASSENAAR, L. I. & NORRIS, D. R. (2017b). Migration distance as a selective episode for wing morphology in a migratory insect. *Movement Ecology* **5**, 1–9.

*FLOCKHART, D. T., PICHANCOURT, J. B., NORRIS, D. R. & MARTIN, T. G. (2015). Unravelling the annual cycle in a migratory animal: breeding−season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology* **84**, 155–165.

*FLOCKHART, D. T., WASSENAAR, L. I., MARTIN, T. G., HOBSON, K. A., WUNDER, M. B. & NORRIS, D. R. (2013). Tracking multi–generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20131087.

*FLUX, J. E. C. (1970). Migration of the butterflies *Glycesthia aurota*, *Catopsilia florella* and *Crenis occidentalum* in East Africa in 1967–68. *Journal of East African Natural History* **119**, 27–29.

*FOX, R. M., LINDSEY, W. A., CLENCH, H. K. & MILLER, L. D. (1965). *The butterflies of Liberia*. American Entomological Society, the Academy of Natural Sciences, Philadelphia, 438 pp.

*FOX, R., BRERETON, T. M., ASHER, J., AUGUST, T. A., BOTHAM, M. S., BOURN, N. A. D., CRUICKSHANKS, K. L., BULMAN, C. R., ELLIS, S., HARROWER, C. A. AND MIDDLEBROOK, I. (2015). *The State of the UK's Butterflies 2015*, Butterfly Conservation, Centre for Ecology & Hydrology, Wareham/Dorset, United Kingdom, 28 pp.

*FOX, R., WARREN, M. S. & BRERETON, T. M. (2010). A new Red List of British Butterflies, *Species Status* **12,** 1–32.

*FREEDMAN, M. G., DINGLE, H., STRAUSS, S. Y. & RAMÍREZ, S. R. (2020). Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. *Proceedings of the National Academy of Sciences* **117**, 28887–28893.

*FREEDMAN, M. G., DINGLE, H., TABULOC, C. A., CHIU, J. C., YANG, L. H. & ZALUCKI, M. P. (2018). Non–migratory monarch butterflies, *Danaus plexippus* (L.), retain developmental plasticity and a navigational mechanism associated with migration. *Biological Journal of the Linnean Society* **123**, 265–278.

*FRENCH, W. L. (1943). Butterfly migration (*Danais melissa dravidarum* and *Euploea core core*). *Journal of the Bombay Natural History Society* **44**, 310.

*FRITZSCHE MCKAY, A., EZENWA, V. O. & ALTIZER, S. (2016). Unravelling the costs of flight for immune defenses in the migratory monarch butterfly. *Integrative and Comparative Biology* **56**, 278–289.

*FROY, O., GOTTER, A. L., CASSELMAN, A. L. & REPPERT, S. M. (2003). Illuminating the circadian clock in monarch butterfly migration. *Science* **300**, 1303–1305.

GAO, B., HEDLUND, J., REYNOLDS, D. R., ZHAI, B. P., HU, G. & CHAPMAN, J. W. (2020). The 'migratory connectivity' concept, and its applicability to insect migrants. *Movement Ecology* **8**, 1–13.

*GARDNER, D. & HOWARTH, B. (2007). A Butterfly migration: blue–spotted Arabs at Jebel Barakah, western Abu Dhabi. *Tribulus* **17**, 98–99.

*GARLAND, M. S. & DAVIS, A. K. (2002). An examination of monarch butterfly (*Danaus plexippus*) autumn migration in coastal Virginia. *The American Midland Naturalist* **147**, 170–174.

*GATEHOUSE, A. G. (1997). Behavior and ecological genetics of wind–borne migration by insects. *Annual Review of Entomology* **42**, 475–502.

*GIBBS, D., WALTON, R., BROWER, L. & DAVIS, A. K. (2006). Monarch butterfly (Lepidoptera: Nymphalidae) migration monitoring at Chincoteague, Virginia and Cape May, New Jersey: a comparison of long–term trends. *Journal of the Kansas Entomological Society* **79**, 156–164.

*GIBBS, G. W. (1969). A large migration of the Australian painted lady butterfly, *Vanessa kershawi* (McCoy), to New Zealand. *New Zealand Entomologist* **4**, 14–21.

*GIBO, D. L. (1993). Notes On *Danaus gilippus* s*trigosus* (Nymphalidae: Danainae) In Southern California. *The Journal of the Lepidopterists' Society* **47**, 160–161.

*GIBO, D. L. (1981). Some observations on soaring flight in the mourning cloak butterfly (*Nymphalis antiopa* L.) in southern Ontario. *Journal of the New York Entomological Society* **89**, 98–101.

*GIBO, D. L. & PALLETT, M. J. (1979). Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. *Canadian Journal of Zoology* **57**, 1393–1401.

*GILBERT, L. E. & SINGER, M. C. (1975). Butterfly ecology. *Annual Review of Ecology, Evolution, and Systematics* **6**, 365–395.

*GLASSBERG, J. (2017). *A swift guide to butterflies of North America*. Princeton University Press, 416 pp.

*GLENDINNING, J. I., MEJIA, A. A. & BROWER, L. P. (1988). Behavioral and ecological interactions of foraging mice (*Peromyscus melanotis*) with overwintering monarch butterflies (*Danaus plexippus*) in Mexico. *Oecologia* **75**, 222–227.

*GRANT, T. J., PARRY, H. R., ZALUCKI, M. P. & BRADBURY, S. P. (2018). Predicting monarch butterfly (*Danaus plexippus*) movement and egg–laying with a spatially–explicit agent–based model: The role of monarch perceptual range and spatial memory. *Ecological Modelling* **374**, 37–50.

*GREEN, D. A., DUAN, Y. & KRONFORST, M. (2017). Investigating the Role of Insulin/IGF Signaling in Determining Migration Traits in the Monarch Butterfly. *Integrative and Comparative Biology* **57**, 278.

*GREHAN, J. R. (1996). *Butterflies of the Green Mountain National Forest*. US Department of Agriculture, Forest Service, 42 pp.

*GUERRA, P. A. & REPPERT, S. M. (2015). Sensory basis of lepidopteran migration: focus on the monarch butterfly. *Current Opinion in Neurobiology* **34**, 20–28.

*GUERRA, P. A., GEGEAR, R. J. & REPPERT, S. M. (2014). A magnetic compass aids monarch butterfly migration. *Nature Communications* **5**, 1–8.

*GUERRA, P. A. & REPPERT, S. M. (2013). Coldness triggers northward flight in remigrant monarch butterflies. *Current Biology* **23**, 419–423.

*GUERRA, P. A., MERLIN, C., GEGEAR, R. J. & REPPERT, S. M. (2012). Discordant timing between antennae disrupts sun compass orientation in migratory monarch butterflies. *Nature Communications* **3**, 1–7.

*GUSTAFSSON, K. M. (2017). Narrating the monarch butterfly: Managing knowledge complexity and uncertainty in coproduction of a collective narrative and public discourse. *Science Communication* **39**, 492–519.

*GWINNER, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology* **199**, 39–48.

*HABER, W. A. (1993). Seasonal migration of monarchs and other butterflies in Costa Rica. In *The Biology and conservation of the monarch butterfly* (eds S. B. Malcolm & M. P. Zalucki), Natural History Museum of Los Angeles County, Los Angeles, CA, pp. 201–207.

*HADDAD, N. M., HUDGENS, B., DAMIANI, C., GROSS, K., KUEFLER, D. & POLLOCK, K. (2008). Determining optimal population monitoring for rare butterflies. *Conservation Biology* **22**, 929–940.

*HANLEY, D., MILLER, N. G., FLOCKHART, D. T. & NORRIS, D. R. (2013). Forewing pigmentation predicts migration distance in wild–caught migratory monarch butterflies. *Behavioral Ecology* **24**, 1108–1113.

*HANSKI, I. & THOMAS, C. D. (1994). Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* **68**, 167–180.

*HANSKI, I., ALHO, J. & MOILANEN, A. (2000). Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**, 239–251.

*HANSKI, I., BREUKER, C. J., SCHÖPS, K., SETCHFIELD, R. & NIEMINEN, M. (2002). Population history and life history influence the migration rate of female Glanville fritillary butterflies. *Oikos* **98**, 87–97.

*HARRIS, A. C. (1988). A large migration of the Australian meadow argus butterfly Junonia villida calybe (Lepidoptera; Nymphalidae) to southern New Zealand. *New Zealand Entomologist* **11**, 67–68.

*HARRIS, J. B. C., REID, J. L., SCHEFFERS, B. R., WANGER, T. C., SODHI, N. S., FORDHAM, D. A. & BROOK, B. W. (2012). Conserving imperiled species: a comparison of the IUCN Red List and US Endangered Species Act. *Conservation Letters* **5**, 64–72.

*HARRISON, S. (1989). Long−distance dispersal and colonization in the bay checkerspot butterfly, Euphydryas editha bayensis. *Ecology* **70**, 1236–1243.

*HAYWARD, K. J. (1925). Migration of Butterflies. *Entomologist* **58**, 169–170.

*HAYWARD, K. J. (1953). Migration of butterflies in Argentina during the spring and summer of 1951−52. *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* **28**, 63–73.

*HAYWARD, K. J. (1967). Notes on Argentine butterfly migration, 1965–66. *Entomologist* **100**, 29–34.

*HEINO, M. & HANSKI, I. (2001). Evolution of migration rate in a spatially realistic metapopulation model. *The American Naturalist* **157**, 495–511.

*HEITZMAN, J. R. (1970). A new US butterfly record and a migration of Eunica monima in Texas. *Mid–Continent Lepidoptera Series* **12**, 10–11.

*HERMAN, W. S. & TATAR, M. (2001). Juvenile hormone regulation of longevity in the migratory monarch butterfly. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 2509–2514.

*HERNÁNDEZ, L. R., SMITH, D. S., DAVIES, N. & ARECES–MALLEA, A. (1994). The butterflies and vegetational zones of Guanahacabibes National Park, Cuba. *Bulletin of the Allyn Museum* **139**, 1–19.

HICKLING, R., ROY, D. B., HILL, J. K., FOX, R. & THOMAS, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* **12**, 450–455.

*HILL, J. K., HAMER, K., TANGAH, J. & DAWOOD, M. (2001). Ecology of tropical butterflies in rainforest gaps. *Oecologia* **128**, 294–302.

*HINGSTON, R. W. G. (1928). *Problems of Instinct and Intelligence among Tropical Insects*. Edward Arnold, London, 296 pp.

*HOBSON, K. A. & NORRIS, D. R. (2008). Animal migration: a context for using new techniques and approaches. *Terrestrial Ecology* **2**, 1–19.

*HOBSON, K. A. (2005). Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk* **122**, 1037–1048.

*HOBSON, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**, 314–326.

*HOBSON, K. A., WASSENAAR, L. I. & TAYLOR, O. R. (1999). Stable isotopes (δD and δ 13 C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* **120**, 397–404.

*HOLDREN, C. E. & EHRLICH, P. R. (1981). Long range dispersal in checkerspot butterflies: transplant experiments with *Euphydryas gillettii*. *Oecologia* **50**, 125–129.

*HOLLAND, R. A., WIKELSKI, M. & WILCOVE, D. S. (2006). How and why do insects migrate?. *Science* **313**, 794–796.

*HOLMES, B. (2008). How monarchs keep on straight and narrow. *New Scientist* **197**, 9.

*HOLYOAK, M., CASAGRANDI, R., NATHAN, R., REVILLA, E. & SPIEGEL, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060–19065.

HOPKINS, T. L. (2005). Extinction of the rocky mountain locust. *BioScience* **55**, 80–82.

*HOTH, J., MERINO, L., OBERHAUSER, K., PISANTY, I., PRICE, S. & WILKINSON, T. (1997). 1997 *North American conference on the monarch butterfly*. U.S. Fish and Wildlife Service, 428 pp.

*HOWARD, E. & DAVIS, A. K. (2015). Investigating long–term changes in the spring migration of monarch butterflies (Lepidoptera: Nymphalidae) using 18 years of data from Journey North, a citizen science program. *Annals of the Entomological Society of America* **108**, 664–669.

*HOWARD, E. & DAVIS, A. K. (2011). A simple numerical index for assessing the spring migration of monarch butterflies using data from Journey North, a citizen–science program. *The Journal of the Lepidopterists' Society* **65**, 267–270.

*HOWARD, E. & DAVIS, A. K. (2009). The fall migration flyways of monarch butterflies in eastern North America revealed by citizen scientists. *Journal of Insect Conservation* **13**, 279–286.

HU, G., LIM, K. S., HORVITZ, N., CLARK, S. J., REYNOLDS, D. R., SAPIR, N. & CHAPMAN, J. W. (2016). Mass seasonal bioflows of high–flying insect migrants. *Science* **354**, 1584–1587.

*HU, G., LIM, K. S., REYNOLDS, D. R., REYNOLDS, A. M. & CHAPMAN, J. W. (2016). Wind–related orientation patterns in diurnal, crepuscular and nocturnal high–altitude insect migrants. *Frontiers in Behavioral Neuroscience* **10**, 32.

*HUNT, E. & TONGEN, A. (2017). A periodic matrix population model for monarch butterflies. *Natural Resource Modeling* **30**, e12123.

*INAMINE, H., ELLNER, S. P., SPRINGER, J. P. & AGRAWAL, A. A. (2016). Linking the continental migratory cycle of the monarch butterfly to understand its population decline. *Oikos* **125**, 1081–1091.

*IRUNGBAM, J. S., MEITEI, L. R., HUIDROM, H., SOIBAM, B. S., NGANGOM, A., NGANGOM, B., MEITEI, R. & FRIC, Z. F. (2020). An inventory of the butterflies of Manipur, India (Insecta: Lepidoptera). *Zootaxa* **4882**, 1–91.

IWAMURA, T., FULLER, R. A. & POSSINGHAM, H. P. (2014). Optimal management of a multispecies shorebird flyway under sea−level rise. *Conservation Biology* **28**, 1710–1720.

*JACKSON, B. S. (1976). Records of the American painted lady in Newfoundland. *Canadian Field–Naturalist* **90**, 492–495.

*JAMDAR, N. (1991). On the migration of the large cabbage white butterfly *Pieris brassicae* in Kashmir. *Journal of the Bombay Natural History Society* **88**, 128–129.

*JAMES, D. G. (1993). Migration biology of the monarch butterfly in Australia. In *The Biology and conservation of the monarch butterfly* (eds S. B. Malcolm & M. P.

Zalucki), Natural History Museum of Los Angeles County, Los Angeles, CA, pp. 189–200.

*JENKINS, D. W. (1990). Neotropical Nymphalidae VIII. Revision of *Eunica*. *Bulletin of the Allyn Museum* **131**, 1–179.

*JENKINS, D. W. (1984). Neotropical Nymphalidae, II. Revision of *Myscelia*. *Bulletin of the Allyn Museum* **87**, 1–64.

*JENKINS, D. W. (1983). Neotropical Nymphalidae I. Revision of *Hamadryas*. *Bulletin of the Allyn Museum* **81**, 1–147.

*JESSE, L. C. H. & OBRYCKI, J. J. (2000). Field deposition of Bt transgenic corn pollen: lethal effects on the monarch butterfly. *Oecologia* **125**, 241–248.

*JIGGINS, C. D. & DAVIES, N. (1998). Genetic evidence for a sibling species of *Heliconius charithonia* (Lepidoptera; Nymphalidae). *Biological Journal of the Linnean Society* **64**, 57–67.

*JOHN, E., WIEMERS, M., MAKRIS, C. & RUSSELL, P. (2013). The *Pontia daplidice* (Linnaeus, 1758) *Pontia edusa* (Fabricius, 1777) complex (Lepidoptera: Pieridae): confirmation of the presence of *Pontia daplidice* in Cyprus, and of *Cleome iberica* DC. as a new host–plant for this species in the Levant. *Entomologist's Gazette* **64**, 69–78.

*JOHN, E., COUTSIS, J. G. & MAKRIS, C. (2006). A review of records for *Colias erate* (Esper, [1805]) (Lep.: Papilionoidea Pieridae) in Cyprus: were they all yellow forms of *Colias croceus* (Geoffroy, 1785)?. *Entomologist's Gazette* **57**, 3–12.

*JOHNSON, C. (1963). Physiological factors in insect migration by flight. *Nature* **198**, 423–427.

*JOHNSON, C. G. (1969). *Migration and dispersal of insects by flight*: Methuen And Co. Ltd.; London, 766 pp.

*JONES, R. E., GILBERT, N., GUPPY, M. & NEALIS, V. (1980). Long–distance movement of *Pieris rapae*. *The Journal of Animal Ecology* **49**, 629–642.

*JUHÁSZ, E., GÓR, Á., BALI, D., KERÉKGYÁRTÓ, F., KATONA, G. & VÉGVÁRI, Z. (2020). Long–term temporal patterns in flight activities of a migrant diurnal butterfly. *Insect Science* DOI 10.1111/1744–7917.12815.

*KANAZAWA, I., CHENG, W. W. W., PUN, H. S. F., SAKIYAMA, Y. & DOI, H. (2015). First migration record of Chestnut Tiger Butterfly, *Parantica sita niphonica* (Moore, 1883) (Lepidoptera: Nymphalidae: Danainae) from Japan to Hong Kong and longest recorded movement by the species. *The Pan–Pacific Entomologist* **91**, 91–97.

*KANTOLA, T., TRACY, J. L., BAUM, K. A., QUINN, M. A. & COULSON, R. N. (2019). Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor. *Biological Conservation* **231**, 150–160.

*KAWAHARA, A. Y. (2006a). Biology of the snout butterflies (Nymphalidae, Libytheinae): Part 1: *Libythea* Fabricius. *Lepidoptera Science* **57**, 13–33.

*KAWAHARA, A. Y. (2006b). Biology of the snout butterflies (Nymphalidae, Libytheinae): Part 2: *Libytheana* Michener. *Lepidoptera Science* **57**, 265–277.

*KELLY, J. F., JOHNSON, M. J., LANGRIDGE, S. & WHITFIELD, M. (2008). Efficacy of stable isotope ratios in assigning endangered migrants to breeding and wintering sites. *Ecological Applications* **18**, 568–576.

*KENDALL, R. O. (1984). Some new and rare records of Lepidoptera found in Texas. *Bulleting of the Allyn Museum* **86**, 1–51.

*KENDALL, R. O. (1976). Larval Foodplants for Thirty Species of Skippers (Lepidoptera, Hesperiidae) from Mexico. *Bulleting of the Allyn Museum* **39**, 1–9.

*KENNEDY, J. S. (1985). Migration, behavioral and ecological. In *Migration : Mechanisms and Adaptive Significance*. Contributions in Marine Science Supplement Vol 27 (ed M. A. Rankin), University of Texas Press, pp. 5–26.

KIRBY, J. S., STATTERSFIELD, A. J., BUTCHART, S. H., EVANS, M. I., GRIMMETT, R. F., JONES, V. R., O'SULLIVAN, J., TUCKER, G. M. & NEWTON, I. (2008). Key conservation issues for migratory land–and waterbird species on the world's major flyways. *Bird Conservation International* **18**, S49–S73.

*KITCHING, R. L. & SCHEERMEYER, E. (1993). The comparative biology and ecology of the Australian danaines. In *The Biology and conservation of the monarch butterfly* (eds S. B. Malcolm & M. P. Zalucki), Natural History Museum of Los Angeles County, Los Angeles, CA, pp. 165–175.

*KITCHING, R. L., SCHEERMEYER, E. & JONES, R. E. (1999). *Biology of Australian butterflies*. CSIRO Publishing, 422 pp.

*KITCHING, R. L. & ZALUCKI, M. P. (1981). Observations on the Ecology of *Euploea core corinna* (Nymphalidae) With Special Reference to an Overwintering Population. *Journal of the Lepidopterists Society* **35**, 106–119.

*KNIGHT, A., BROWER, L. P. & WILLIAMS, E. H. (1999). Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north–central Florida: estimating population parameters using mark–recapture. *Biological Journal of the Linnean Society* **68**, 531–556.

*KNIGHT, S. M., PITMAN, G. M., FLOCKHART, D. T. & NORRIS, D. R. (2019). Radio–tracking reveals how wind and temperature influence the pace of daytime insect migration. *Biology Letters* **15**, 20190327.

KOH, L. P. & SODHI, N. S. (2004). Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications* **14**, 1695–1708.

*KUNTE, K. (2005). Species composition, sex–ratios and movement patterns in danaine butterfly migrations in southern India. *Journal of the Bombay Natural History Society* **102**, 280–286.

*KUUSSAARI, M., NIEMINEN, M. & HANSKI, I. (1996). An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of animal Ecology* **65**, 791–801.

*LACK, E. (1951). Migration of insects and birds through a Pyrenean pass. *The Journal of Animal Ecology* **20**, 63–67.

*LAM, F. C., BRUINSMA, M. & MELLES, G. R. (2014). Descemet membrane endothelial transfer. *Current Opinion in Ophthalmology* **25**, 353–357.

*LAMBKIN, T. A., BRABY, M. F., EASTWOOD, R. G. & ZALUCKI, M. P. (2019). Taxonomic revision of the *Euploea alcathoe* complex (Lepidoptera: Nymphalidae) from Australia and New Guinea. *Austral Entomology* **58**, 52–75.

*LARSEN, K. J. & LEE JR, R. E. (1994). Cold tolerance including rapid cold–hardening and inoculative freezing of fall migrant monarch butterflies in Ohio. *Journal of Insect Physiology* **40**, 859–864.

*LARSEN, T. B. (2005a). *Butterflies of West Africa*. Apollo Books, 865 pp.

*LARSEN, T. B., VAN HAO, L. & VAN LAP, D. (2005b). Butterfly diversity in Cuc Phuong National Park, Viet Nam. *Biodiversity* **6**, 3–14.

*LARSEN, T. B. (2004). *Butterflies of Bangladesh: an annotated checklist*, IUCN, the World Conservation Union, Bangladesh Country Office, 158 pp.

*LARSEN, T. B. (1997). *Papilio camillus* Fabricius, 1781 (currently *Cyrestis camillus*) and *Limenitis reducta* Staudinger, 1901 (Insecta, Lepidoptera): proposed conservation of the specific names. *Bulletin of Zoological Nomenclature* **54**, 155–158.

*LARSEN, T. B. (1995). A large–scale migration of the African skipper *Andronymus gander* Evans, 1946 near Calabar, Nigeria (Lepidoptera: Hesperiidae). *Entomologists' Record and Journal of Variation* **107**, 263–266.

*LARSEN, T. B. (1992a). The Butterflies of the Gemsbok National Park in Botswana (Lepidoptera–Rhopalocera). *Botswana Notes and Records* **24**, 181–203.

*LARSEN, T. B. (1992b). Temporary prey–specialization on migrant butterflies by bluecheeked bee–eaters. *Entomologists' Record and Journal of Variation* **104**, 253–255.

*LARSEN, T.B. (1992c). A migration of Catopsilia florella (f.) in Botswana; morphological differences between migratory and non–migratory populations (Lepidoptera: Pieridae). *Tropical Lepidoptera* **3**, 3–11.

*LARSEN, T. B. (1991). *The butterflies of Kenya and their natural history*. Oxford University Press, 522 pp.

*LARSEN, T. B. (1988). Butterfly Migration Activity In Southwestern India During September And October Of 1986. *Atalanta* **18**, 283–289.

*LARSEN, T. (1987). The butterflies of the Nilgiri mountains of southern India (Lepidoptera: Rhopalocera). *Journal of the Bombay Natural History Society* **84**, 291–316.

*LARSEN, T. B. (1986). Tropical butterflies of the Mediterranean. *Nota Lepidopterologica* **9**, 63–77.

*LARSEN, T. B. (1985). A mixed butterfly migration in the Nairobi area of Kenya. *Atalanta* **16**, 104–105.

*LARSEN, T. B. (1984). *Butterflies of Saudi Arabia and its neighbours*: Stacey International, 160 pp.

*LARSEN, T. B. (1982). The importance of migration to the butterfly fauna of Arabia (Lep., Rhopalocera). *Atalanta* **4**, 248–259.

*LARSEN, T. B.  1978. A mixed butterfly migration in West Africa (Lepidoptera: Rhopalocera), *Atalanta* **9**, 191–199.

*LARSEN, T. B. (1977a). A Migration of *Anaphaeis Aurota* (F.) in Kenya (Lep.: Pieridae). *Deutsche Entomologische Zeitschrift* **24**, 419–422.

*LARSEN, T. B. (1977b). Butterfly Migrations in the Nilgiri Hills of South India (Lepidoptera: Rhopalocera). *Journal of the Bombay Natural History Society* **74**, 546–549.

*LARSEN, T. B. (1975). Provisional notes on migrant butterflies in Lebanon. *Atalanta Munnerstadt* **62**, 62–74.

*LARSEN, T. B. (1968). Butterflies migrating on Ikoyi Island (Lagos). *Nigerian Entomological Magazine* **1**, 62.

*LARSON, B. M. & BARR, S. (2016). The Flights of the Monarch Butterfly: Between In Situ and Ex Situ Conservation. In *Animal Ethics in the Age of Humans* (eds M. K. & P. B. Thompson). Springer, Cham, pp. 355–368.

*LEMOINE, N. P. (2015). Climate change may alter breeding ground distributions of eastern migratory monarchs (*Danaus plexippus*) via range expansion of *Asclepias* host plants. *PLoS One* **10**, e0118614.

*LIEDVOGEL, M., ÅKESSON, S. & BENSCH, S. (2011). The genetics of migration on the move. *Trends in Ecology & Evolution* **26**, 561–569.

*LOHMANN, K. J. (2018). Animal migration research takes wing. *Current Biology* **28**, R952–R955.

*LÓPEZ–HOFFMAN, L., CHESTER, C. C., SEMMENS, D. J., THOGMARTIN, W. E., RODRÍGUEZ–MCGOFFIN, M. S., MERIDETH, R. & DIFFENDORFER, J. E. (2017). Ecosystem services from transborder migratory species: implications for conservation governance. *Annual Review of Environment and Resources* **42**, 509–539.

*LOSEY, J. E., RAYOR, L. S. & CARTER, M. E. (1999). Transgenic pollen harms monarch larvae. *Nature* **399**, 214–214.

*LUKHTANOV, V. A., PAZHENKOVA, E. A. & NOVIKOVA, A. V. (2016). Mitochondrial chromosome as a marker of animal migratory routes: DNA barcoding revealed Asian (non–African) origin of a tropical migrant butterfly Junonia orithya in south Israel. *Comparative Cytogenetics* **10**, 671.

*LUNDMARK, C. (2010). Long–distance insect migration. *BioScience* **60**, 400–400.

*MACKINNON, P. W. & DE NICÉVILLE, L. (1899). List of butterflies of Mussoorie in the Western Himalayas and neighbouring regions. *Journal of the Bombay Natural History Society* **11**, 205–221.

*MALCOLM, S. B. (2018). Anthropogenic impacts on mortality and population viability of the monarch butterfly. *Annual Review of Entomology* **63**, 277–302.

*MALCOLM, S.B. & SLAGER, B. H. (2015). Migration and host plant use by the southern monarch, *Danaus erippus*. In *Monarchs in a changing world: Biology and conservation of an iconic butterfly* (eds K. A. Oberhauser, K. R. Nail & S. Altizer), Cornell University Press, Ithaca, N.Y., USA, pp. 225–235.

*MALCOLM, S. B., COCKRELL, B. J. & BROWER, L. P. (1993). Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? In *Biology and Conservation of the Monarch Butterfly* (eds S. B. Malcolm and M. P. Zalucki), Natural History Museum of Los Angeles County, pp. 253–267.

*MALCOLM, S. B. (1987). Monarch butterfly migration in North America: Controversy and conservation. *Trends in Ecology & Evolution* **2**, 135–138.

*MANIL, L. & CUVELIER, S. *Nymphalis xanthomelas* (Esper, 1781) Mass migration, temporary colonisation or sustainable expansion?. *Phegea* **58**, 69–74.

*MARÍN, L., LEÓN–CORTÉS, J. L. & STEFANESCU, C. (2009). The effect of an agro–pasture landscape on diversity and migration patterns of frugivorous butterflies in Chiapas, Mexico. *Biodiversity and Conservation* **18**, 919–934.

*MARINI, L. & ZALUCKI, M. P. (2017). Density–dependence in the declining population of the monarch butterfly. *Scientific Reports* **7**, 1–8.

MARTIN, T. G., CHADÈS, I., ARCESE, P., MARRA, P. P., POSSINGHAM, H. P. & NORRIS, D. R. (2007). Optimal conservation of migratory species. *PloS One* **2**, e751.

*MATHAVAN, S. & PANDIAN, T. J. (1975). Effect of temperature on food utilization in the monarch butterfly *Danaus chrysippus*. *Oikos* **26**, 60–64.

*MATHEW, G. & BINOY, C. F. (2002). Migration of butterflies (Lepidoptera: Rhopalocera) in the new Amarambalam reserve forest of the Nilgiri biosphere reserve. *Zoos' Print* **17**, 844–847.

*MATTER, S. F. (2006). Changes in landscape structure decrease mortality during migration. *Oecologia* **150**, 8–16.

*MATTER, S. F., ROSLIN, T. & ROLAND, J. (2005). Predicting immigration of two species in contrasting landscapes: effects of scale, patch size and isolation. *Oikos* **111**, 359–367.

*MATTER, S. F., ROLAND, J., MOILANEN, A. & HANSKI, I. (2004). Migration and survival of *Parnassius smintheus*: detecting effects of habitat for individual butterflies. *Ecological Applications* **14**, 1526–1534.

*MATTER, S. F., ROLAND, J., KEYGHOBADI, N. & SABOURIN, K. (2003). The effects of isolation, habitat area and resources on the abundance, density and movement of the butterfly *Parnassius smintheus*. *The American Midland Naturalist* **150**, 26–36.

*MCCANN, C. (1943). A "busman's" Holiday in the Abu Hills. Journal of The Bombay Natural History Society **43**, 206–217.

*MCCORD, J. W. & DAVIS, A. K. (2010). Biological observations of monarch butterfly behavior at a migratory stopover site: results from a long–term tagging study in coastal South Carolina. *Journal of Insect Behavior* **23**, 405–418.

*MCKENNA, D. D., MCKENNA, K. M., MALCOLM, S. B. & BERENBAUM, M. (2001). Mortality of Lepidoptera along roadways in central Illinois. *The Journal of the Lepidopterists Society* **55**, 63–68.

*MCKILLOP, W. B., PRESTON, W. B. & WESTWOOD, A. R. (1992). Range extension for the European skipper, *Thymelicus lineola* (Ochsenheimer), 1808 (Lepidoptera: Hesperiidae), in Manitoba. *The Canadian Entomologist* **124**, 943–944.

*MEERMAN, J. C. & BOOMSMA, T. (1997). *Urania fulgens* and other Lepidoptera migrations in Belize, Central America. *News of the Lepidopterists' Society* **39**, 8–9.

*MEITNER, C. J., BROWER, L. P. & DAVIS, A. K. (2004). Migration patterns and environmental effects on stopover of monarch butterflies (Lepidoptera, Nymphalidae) at Peninsula Point, Michigan. *Environmental Entomology* **33**, 249–256.

*MELERO, Y., STEFANESCU, C. & PINO, J. (2016). General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biological Conservation* **201**, 336–342.

*MENZ, M., REYNOLDS, D. R., GAO, B., HU, G., CHAPMAN, J. & WOTTON, K. (2019). Mechanisms and consequences of partial migration in insects. *Frontiers in Ecology and Evolution* **7**, 1–9.

*MERLIN, C., HEINZE, S. & REPPERT, S. M. (2012). Unraveling navigational strategies in migratory insects. *Current Opinion in Neurobiology* **22**, 353–361.

*MIGDOLL, I. (1988). *Field guide to the butterflies of southern Africa*. New Holland Press, 256 pp.

*MIKKOLA, K. (2003). Red admirals *Vanessa atalanta* (Lepidoptera: Nymphalidae) select northern winds on southward migration. *Entomologica Fennica* **14**, 15–24.

*MILIUS, S. (2004). Thoroughly modern migrants: Moths and butterflies—round−trip tickets not necessary. *Science News* **165**, 408–410.

*MILLER, N. G., WASSENAAR, L. I., HOBSON, K. A. & NORRIS, D. R. (2012). Migratory connectivity of the monarch butterfly (*Danaus plexippus*): patterns of spring re–colonization in eastern North America. *PLoS One* **7**, e31891.

*MILLER, J. C. & Hammond, P. C. (2007). *Butterflies and moths of Pacific Northwest forests and woodlands: rare, endangered, and management–sensitive species*. Forest Health Technology Enterprise Team, 243 pp.

*MILLER, S. E. (1985). Butterflies of the California Channel islands. *Journal of Research on the Lepidoptera* **23**, 282–296.

*MILLER, L. D. (1979). Studies in the Lycaeninae (Lycaenidae). *Bulletin of the Allyn Museum* **51**, 1–30.

*MILLS, S. C., OLIVER, T. H., BRADBURY, R. B., GREGORY, R. D., BRERETON, T., KÜHN, E., ... & EVANS, K. L. (2017). European butterfly populations vary in sensitivity to weather across their geographical ranges. *Global Ecology and Biogeography* **26**, 1374–1385.

*MILNE, B. G. (1964). A migration of *Belenois aurota* F., and *Catopsilia florella* L. (Lepidoptera: Pieridae) in the Transvaal. *Journal of the Entomological Society of Southern Africa* **27**, 37–42.

*MILNER–GULLAND, E., FRYXELL, J. M. & SINCLAIR, A. R. (2011). *Animal migration: a synthesis*, Oxford University Press, 280 pp.

*MINTER, M., PEARSON, A., LIM, K. S., WILSON, K., CHAPMAN, J. W. & JONES, C. M. (2018). The tethered flight technique as a tool for studying life−history strategies associated with migration in insects. *Ecological Entomology* **43**, 397–411.

*MORANZ, R. & BROWER, L. P. (1998). Geographic and temporal variation of cardenolide–based chemical defenses of queen butterfly (*Danaus gilippus*) in northern Florida. *Journal of Chemical Ecology* **24**, 905–932.

*MOSKOWITZ, D., MOSKOWITZ, J., MOSKOWITZ, S. & MOSKOWITZ, H. (2001). Notes on a large dragonfly and butterfly migration in New Jersey. *Northeastern Naturalist* **8**, 483–490.

*MOURITSEN, H. (2018). Long–distance navigation and magnetoreception in migratory animals. *Nature* **558**, 50–59.

*MOURITSEN, H., DERBYSHIRE, R., STALLEICKEN, J., MOURITSEN, O. Ø., FROST, B. J. & NORRIS, D. R. (2013a). An experimental displacement and over 50 years of tag–recoveries show that monarch butterflies are not true navigators. *Proceedings of the National Academy of Sciences* **110**, 7348–7353.

*MOURITSEN, H., DERBYSHIRE, R., STALLEICKEN, J., MOURITSEN, O. Ø., FROST, B. J. & NORRIS, D. R. (2013b). An experimental displacement and over 50 years of tag–recoveries show that monarch butterflies are not true navigators. *Proceedings of the National Academy of Sciences* **110**, 7348–7353.

*MOURITSEN, H. & FROST, B. J. (2002). Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proceedings of the National Academy of Sciences* **99**, 10162–10166.

*MYRES, M. T. (1985). A southward return migration of painted lady butterflies, *Vanessa cardui*, over southern Alberta in the fall of 1983, and biometeorological aspects of their outbreaks into North America and Europe. *Canadian Field–Naturalist* **99**, 147–155.

*NAIR, V. P. (2007). A new larval food plant of the common albatross *Appias albina* (Boisduval), with a note on its migration in Kerala, *Journal of the Bombay Natural History Society* **104**, 366.

*NAKASUJI, F. & NAKANO, A. (1990). Flight activity and oviposition characteristics of the seasonal form of a migrant skipper, *Parnara guttata guttata* (Lepidoptera: Hesperiidae). *Population Ecology* **32**, 227–233.

*NAKONIECZNY, M., KEDZIORSKI, A. & MICHALCZYK, K. (2007). Apollo butterfly (*Parnassius apollo* L.) in Europe–its history, decline and perspectives of conservation. *Functional Ecosystems and Communities* **1**, 56–79.

*NATHAN, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* **105**, 19050–19051.

*NATHAN, R., PERRY, G., CRONIN, J. T., STRAND, A. E. & CAIN, M. L. (2003). Methods for estimating long−distance dispersal. *Oikos* **103**, 261–273.

*NATHANSON, F. E. & REILLY, J. P. (1968). Radar Precipitation Echoes Experiments on Temporal, Spatial, and Frequency Correlation. *IEEE Transactions on Aerospace and Electronic Systems* **4**, 505–514.

*NESBIT, R., HILL, J., WOIWOD, I., SIVELL, D., BENSUSAN, K. & CHAPMAN, J. (2009). Seasonally adaptive migratory headings mediated by a sun compass in the painted lady butterfly, *Vanessa cardui*. *Animal Behaviour* **78**, 1119–1125.

NEW, T. (1997). Are Lepidoptera an effective ‘umbrella group ‘for biodiversity conservation? *Journal of Insect Conservation* **1**, 5–12.

*NEW, T. R., BUSH, M. B., THORNTON, I. B. & SUDARMAN, H. K. (1988). The butterfly fauna of the Krakatau Islands after a century of colonization. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* **322**, 445–457.

*NEW, T. R., BUSH, M. B. & SUDARMAN, H. K. (1987). Butterflies from the Ujung Kulon national park, Indonesia. *Journal of the Lepidopterists' Society* **41**, 29–40.

*NEW, T. R., FARRELL, G. S., HIVES, N. W. & HORNE, P. A. (1985). An early season migration of *Catopsilia pomona* (Lepidoptera: Pieridae) in Java, Indonesia. *Journal of Research on the Lepidoptera* **24**, 84–85.

*NISHIDA, K., NAKAMURA, I. & MORALES, C. O. (2009). Plants and butterflies of a small urban preserve in the Central Valley of Costa Rica. *Revista de Biología Tropical* **57**, 31–67.

*OBERHAUSER, K., WIEDERHOLT, R., DIFFENDORFER, J. E., SEMMENS, D., RIES, L., THOGMARTIN, W. E., LOPEZ−HOFFMAN, L. & SEMMENS, B. (2017). A trans−national monarch butterfly population model and implications for regional conservation priorities. *Ecological Entomology* **42**, 51–60.

*OBERHAUSER, K. S., NAIL, K. R. & ALTIZER, S. (2015). *Monarchs in a changing world: biology and conservation of an iconic butterfly*, Cornell University Press, 336 pp.

*OBERHAUSER, K. S. & SOLENSKY, M. J. (2004). *Monarch butterfly biology & conservation*. Cornell university press, 248 pp.

*OBERHAUSER, K. & PETERSON, A. T. (2003). Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences* **100,** 14063–14068.

*O'BYRNE, H. (1939). Notes on butterfly migration. *Bulletin of the Brooklyn Entomological Society* **34**, 252–254.

*O'BYRNE, H. (1933). A Migratory Flight of *Catopsilia Eubule* (Lepid.: Pieridæ). *Psyche* **40**, 131–136.

*O'BYRNE, H. (1932). Notes on butterfly migration. *Bulletin of the Brooklyn Entomological Society* **27**, 185–188.

*ODENDAL, F. J. & EHRLICH, P. R. (1985). A migration of *Urania fulgens* (Uraniidae) in Costa Rica. *Biotropica* **17**, 46–49.

*ODERMATT, J., FROMMEN, J. G. & MENZ, M. H. (2017). Consistent behavioural differences between migratory and resident hoverflies. *Animal Behaviour* **127**, 187–195.

*OLIVEIRA, E. G., SRYGLEY, R. B. & DUDLEY, R. O. B. E. R. T. (1998). Do neotropical migrant butterflies navigate using a solar compass?. *Journal of Experimental Biology*, **201**, 3317–3331.

*ORMISTON, W. (1918). Notes on Ceylon Butterflies [in Spolia Zeylanica, Issue from The Colombo Museum, Ceylon (eds C. T. Symons & W. A. Cave), Government Printer, Colombo, Ceylon, 84 pp.

*ORMISTON, W. (2003). *The Butterflies of Ceylon*. Asian Educational Services, 201 pp.

*ORR, A. G. (1992). Observations on the biology of migrating *Euploea* butterflies in North West Borneo. *The Raffles Bulletin of Zoology* **40**, 221–228.

*OVASKAINEN, O., SMITH, A. D., OSBORNE, J. L., REYNOLDS, D. R., CARRECK, N. L., MARTIN, A. P., ... & HANSKI, I. (2008). Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *Proceedings of the National Academy of Sciences* **105**, 19090–19095.

*OWEN, D. F. & WIEGERT, R. G. (1985). A southward movement of the painted lady butterfly in Wyoming. *The Southwestern Naturalist* **30**, 158–159.

*OWEN, D. F. (1971). *Tropical butterflies. The ecology and behaviour of butterflies in the tropics with special reference to African species*. Oxford, Clarendon Press, 214 pp.

*PAGEL, M. & PAYNE, R. J. (1996). How migration affects estimation of the extinction threshold. *Oikos* **76**, 323–329.

*PALO, J., VARVIO, S. L., HANSKI, I. & VÄINÖLÄ, R. (1995). Developing Microsatellite Markers for Insect Population Structure: Complex Variation in a Checkerspot Butterfly. *Hereditas* **123**, 295–300.

*PALOT, M. J. (2012). A note on the migration of Dark Cerulean *Jamides bochus* (Stoll) (Lepidoptera: Lycaenidae) in Eravikulam National Park, Idukki District, Kerala, India. *Journal of Threatened Taxa* **4**, 3373–3374.

PARMESAN, C., RYRHOLM, N., STEFANESCU, C., HILL, J. K., THOMAS, C. D., DESCIMON, H., HUNTLEY, B., KAILA, L., KULLBERG, J. & TAMMARU, T. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583.

*PARSONS, R. E. (1947). Migration of the butterfly *Appias albina danada*. *Journal of the Bombay Natural History Society*, **47**, 394–396.

*PENNISI, E. (2003). Monarchs check clock to chart migration route. *Science* **300**, 1216–1218.

*PERKINS, E. M. & MEYER, W. C. (1973). Revision of the *Boloria epithore* complex, with description of two new subspecies (Nymphalidae). *Bulletin of the Allyn Museum* **11**, 1–23.

*PETIT, S., MOILANEN, A., HANSKI, I. & BAGUETTE, M. (2001). Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos* **92**, 491–500.

*PFEILER, E., NAZARIO–YEPIZ, N. O., PÉREZ–GÁLVEZ, F., CHÁVEZ–MORA, C. A., LACLETTE, M. R. L., RENDÓN–SALINAS, E. & MARKOW, T. A. (2017). Population genetics of overwintering monarch butterflies, *Danaus plexippus* (Linnaeus), from central Mexico inferred from mitochondrial DNA and microsatellite markers. *Journal of Heredity* **108**, 163–175.

*PIERCE, A. A., ZALUCKI, M. P., BANGURA, M., UDAWATTA, M., KRONFORST, M. R., ALTIZER, S., HAEGER, J. F. & DE ROODE, J. C. (2014). Serial founder effects and genetic differentiation during worldwide range expansion of monarch butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20142230.

*PLEASANTS, J. M. & OBERHAUSER, K. S. (2017). Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population: Herbicide use and monarch butterflies. *Insect Conservation and Diverstiy* **6**, 135–144.

*PLEASANTS, J. M., ZALUCKI, M. P., OBERHAUSER, K. S., BROWER, L. P., TAYLOR, O. R. & THOGMARTIN, W. E. (2017). Interpreting surveys to estimate the size of the monarch butterfly population: Pitfalls and prospects. *PloS One* **12**, e0181245.

*PLEASANTS, J. M., WILLIAMS, E. H., BROWER, L. P., OBERHAUSER, K. S. & TAYLOR, O. R. (2016). Conclusion of no decline in summer monarch population not supported. *Annals of the Entomological Society of America* **109**, 169–171.

*POLLARD, E., C. A. M. VAN SWAAY, C. STEFANESCU, K. E. LUNDSTEN, D. MAES & J. N. GREATOREX–DAVIES. (1998). Migration of the painted lady butterfly *Cynthia cardui* in Europe: evidence from monitoring. *Diversity and Distributions* **4**, 243–253.

*POLLARD, E., MOSS, D. & YATES, T. J. (1995). Population trends of common British butterflies at monitored sites. *Journal of Applied Ecology* **32**, 9–16.

*POLLARD, E., VAN SWAAY, C. A. M., STEFANESCU, C., LUNDSTEN, K. E., MAES, D. & GREATOREX–DAVIES, J. N. (1998). Migration of the painted lady butterfly *Cynthia cardui* in Europe: evidence from monitoring. *Diversity and Distributions* **4**, 243–253.

*POZO, C., MARTÍNEZ, A. L., TESCUM, S. U., SUÁREZ, N. S. & MARTÍNEZ, A. M. (2003). Butterflies (Papilionoidea and Hesperioidea) of Calakmul, Campeche, México. *The Southwestern Naturalist* **48**, 505–525.

*RABASA, S. G., GUTIÉRREZ, D. & ESCUDERO, A. (2007). Metapopulation structure and habitat quality in modelling dispersal in the butterfly *Iolana iolas*. *Oikos* **116**, 793–806.

*RAMESH, T., HUSSAIN, K. J., SATPATHY, K. & SELVANAYAGAM, M. (2012). A note on annual bidirectional movement of butterflies at South–Eastern plains of India. *Research in Zoology* **2**, 1–6.

*RAMÍREZ, M. I., SÁENZ–ROMERO, C., REHFELDT, G. E. & SALAS–CANELA, L. (2015). Threats to the availability of overwintering habitat in the Monarch Butterfly Biosphere Reserve: land use and climate change. In *Monarchs in a Changing World:*

*Biology and Conservation of an Iconic Butterfly* (eds K. S. Oberhauser, K. R. Nail & S. Altizer), pp 157–168.

*RAMÍREZ, M. I., AZCÁRATE, J. G. & LUNA, L. (2003). Effects of human activities on monarch butterfly habitat in protected mountain forests, Mexico. *The Forestry Chronicle* **79**, 242–246.

*RAMÍREZ–RESTREPO, L. & MACGREGOR–FORS, I. (2017). Butterflies in the city: a review of urban diurnal Lepidoptera. *Urban Ecosystems* **20**, 171–182.

*RAUT, N. B. & PENDHARKAR, A. (2009). Butterfly (Rhopalocera) fauna of Maharashtra Nature Park, Mumbai, Maharashtra, India. *Check List* **6**, 022–025.

*RAWLINS, J. E. & LEDERHOUSE, R. C. (1981). Developmental influences of thermal behavior on monarch caterpillars (*Danaus plexippus*): an adaptation for migration (Lepidoptera: Nymphalidae: Danainae). *Journal of the Kansas Entomological Society* **54**, 387–408.

*REEVE, J. D. (1988). Environmental variability, migration, and persistence in host–parasitoid systems. *The American Naturalist* **132**, 810–836.

REHFELDT, G. E., CROOKSTON, N. L., SÁENZ–ROMERO, C. & CAMPBELL, E. M. (2012). North American vegetation model for land−use planning in a changing climate: a solution to large classification problems. *Ecological Applications* **22**, 119–141.

*REPPERT, S. M. & DE ROODE, J. C. (2018). Demystifying monarch butterfly migration. *Current Biology* **28**, R1009–R1022.

*REPPERT, S. M., GUERRA, P. A. & MERLIN, C. (2016). Neurobiology of monarch butterfly migration. *Annual Review of Entomology* **61**, 25–42.

*REPPERT, S. M., GEGEAR, R. J. & MERLIN, C. (2010). Navigational mechanisms of migrating monarch butterflies. *Trends in Neurosciences* **33**, 399–406.

*REPPERT, S. M., ZHU, H. & WHITE, R. H. (2004). Polarized light helps monarch butterflies navigate. *Current Biology* **14**, 155–158.

REYNOLDS, D. R., CHAPMAN, J. W. & HARRINGTON, R. (2006) The migration of insect vectors of plant and animal viruses. *Advances in Virus Research* **67**, 453–517.

*RIBEIRO, D. B., PRADO, P. I., BROWN JR, K. S. & FREITAS, A. V. (2008). Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. *Diversity and Distributions* **14**, 961–968.

*RICHMAN, D. B. & EDWARDS, G. B. (1976). Feeding by four species of migrating butterflies in northern Florida. *Florida Entomologist* **59**, 304.

*RIES, L., TARON, D. J. & RENDÓN–SALINAS, E. (2015). The disconnect between summer and winter monarch trends for the eastern migratory population: Possible links to differing drivers. *Annals of the Entomological Society of America* **108**, 691–699.

*RIVERA–FLORES, M. A., GONZÁLEZ–GÓMEZ, R., LUNA–SORIA, H. & GARCÍA–RUBIO, O. R. (2015). Using Citizen–Monitoring to Define the Migration Route of Monarch Butterfly, *Danaus plexippus* (L.) 1, in the State of Guanajuato. *Southwestern Entomologist* **40**, 233–236.

*ROBERTSON, G., ZALUCKI, M. & PAINE, T. (2015). Larval host choice of the monarch butterfly (*Danaus plexippus* L.) on four native California desert milkweed species. *Journal of Insect Behavior* **28**, 582–592.

ROBINSON, R. A., CRICK, H. Q., LEARMONTH, J. A., MACLEAN, I. M., THOMAS, C. D., BAIRLEIN, F., FORCHHAMMER, M. C., FRANCIS, C. M., GILL, J. A. & GODLEY, B. J. (2009). Travelling through a warming world: climate change and migratory species. *Endangered Species Research* **7**, 87–99.

*RUBENSTEIN, D. R. & HOBSON, K. A. (2004). From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology & Evolution* **19**, 256–263.

*RUDOLPH, D. C., ELY, C. A., SCHAEFER, R. R., WILLIAMSON, J. H. & THILL, R. E. (2006). Monarch (*Danaus plexippus* L. Nymphalidae) migration, nectar resources and fire regimes in the Ouachita Mountains of Arkansas. *The Journal of the Lepidopterists' Society* **60**, 165–170.

RUIZ VARGAS, N., ROWE, L., STEVENS, J., ARMAGOST, J. E., JOHNSON, A. C. & MALCOLM, S. B. (2018). Sequential partial migration across monarch generations in Michigan. *Animal Migration* **5**, 104–114.

RUNGE, C. A. (2015). *Conserving migratory and nomadic species*. School of Biological Sciences. University of Queensland, Brisbane, Australia, 161 pp.

RUNGE, C. A., MARTIN, T. G., POSSINGHAM, H. P., WILLIS, S. G. & FULLER, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment* **12**, 395–402.

RUNGE, C. A., TULLOCH, A., HAMMILL, E., POSSINGHAM, H. P. & FULLER, R. A. (2015). Geographic range size and extinction risk assessment in nomadic species. *Conservation Biology* **29**, 865–876.

*RUSZCZYK, A., MOTTA, P. C., BARROS, R. L. & ARAÚJO, A. M. (2004). Ecological correlates of polyphenism and gregarious roosting in the grass yellow butterfly *Eurema elathea* (Pieridae). *Brazilian Journal of Biology* **64**, 151–164.

*SÁENZ–ROMERO, C., REHFELDT, G. E., DUVAL, P. & LINDIG–CISNEROS, R. A. (2012). Abies religiosa habitat prediction in climatic change scenarios and implications for monarch butterfly conservation in Mexico. *Forest Ecology and Management* **275**, 98–106.

*SAMMUT, P. (2007). *Cacyreus marshalli* Butler,[1898] reaches the Maltese Islands (Lepidoptera: Lycaenidae). *SHILAP Revista de Lepidopterología* **35**, 317–319.

SÁNCHEZ–BAYO, F. & WYCKHUYS, K. A. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* **232**, 8–27.

*SAPP, G. (1999). *Chasing monarchs: A migration with the butterflies of passage*. Yale University Press, 336 pp.

*SATTERFIELD, D. A., SILLETT, T. S., CHAPMAN, J. W., ALTIZER, S. & MARRA, P. P. (2020). Seasonal insect migrations: massive, influential and overlooked. *Frontiers in Ecology and the Enviornment* **18**, 335–344.

*SATTERFIELD, D. A., MAERZ, J. C., HUNTER, M. D., FLOCKHART, D. T., HOBSON, K. A., NORRIS, D. R., STREIT, H., DE ROODE, & ALTIZER, S. (2018). Migratory monarchs that encounter resident monarchs show life−history differences and higher rates of parasite infection. *Ecology Letters* **21**, 1670–1680.

*SATTERFIELD, D. A., ALTIZER, S., WILLIAMS, M. K. & HALL, R. J. (2017). Environmental persistence influences infection dynamics for a butterfly pathogen. *PloS One* **12**, e0169982.

*SATTERFIELD, D. A. & ALTIZER, S. (2016a). Monarchs as a model system to understand mechanisms linking animal migration and infectious disease dynamics. *Integrative and Comparative Biology* **56**, E194–E194.

*SATTERFIELD, D. A., VILLABLANCA, F. X., MAERZ, J. C. & ALTIZER, S. (2016b). Migratory monarchs wintering in California experience low infection risk compared to monarchs breeding year–round on non–native milkweed. *Integrative and Comparative Biology* **56**, 343–352.

*SATTERFIELD, D. A., MAERZ, J. C. & ALTIZER, S. (2015). Loss of migratory behaviour increases infection risk for a butterfly host. *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 20141734.

*SAUMAN, I., BRISCOE, A. D., ZHU, H., SHI, D., FROY, O., STALLEICKEN, J., YUAN, Q., CASSELMAN, A. & REPPERT, S. M. (2005). Connecting the navigational clock to sun compass input in monarch butterfly brain. *Neuron* **46**, 457–467.

*SAUNDERS, S. P., RIES, L., OBERHAUSER, K. S. & ZIPKIN, E. F. (2016). Evaluating confidence in climate−based predictions of population change in a migratory species. *Global Ecology and Biogeography* **25**, 1000–1012.

*SCHAEFER, G. W. (1969). Radar studies of locust, moth and butterfly migration in the Sahara. *Proceedings of the Royal Society of London C* **34**, 39–40.

*SCHEERMEYER, E. (1993). Overwintering of three Australian danaines: *Tirumala hamata hamata*, *Euploea tulliolus tulliolus*, and *E. core corinna*. *The Biology and conservation of the monarch butterfly* (eds S. B. Malcolm & M. P. Zalucki), Natural History Museum of Los Angeles County, Los Angeles, CA, 345–354 pp.

*SCHEERMEYER, E. (1987). *Seasonality or opportunism in reproduction of Australian danaine butterflies: Euploea core, E. tulliolus and Tirumala hamata (Lepidoptera)* Griffith University, 309 pp.

*SCHEERMEYER, E. (1985). Some Factors Affecting the Distribution of *Euploea Core Corinna* (Ws Macleay) (Lepidoptera: Danainae). *Australian Journal of Zoology* **33**, 339–348.

*SCHULTZ, C. B. (1998). Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* **12**, 284–292.

*SCHWANWITSCH, B. N. (1928). Studies upon the wing–pattern of *Pierella* and related genera of South American satyridan butterflies. *Zeitschrift für Morphologie und Ökologie der Tiere* **10**, 433–532.

*SCOTT, J. A. (1972). Biogeography of Antillean butterflies. *Biotropica* **4**, 32–45.

*SCRIBER, J. M., TSUBAKI, Y. & LEDERHOUSE, R. C. (1995). *Swallowtail butterflies: their ecology and evolutionary biology*, Scientific Publishers, Gainesville, FL, 459 pp.

*SCUDDER, S. H. (1889). *The butterflies of the eastern United States and Canada: with special reference to New England*. Cambridge, Ma, 1958 pp.

*SCUDDER, S. H. (1876). A Cosmopolitan Butterfly. II. Its History. *The American Naturalist* **10**, 602–611.

*SEARS, M. K., HELLMICH, R. L., STANLEY–HORN, D. E., OBERHAUSER, K. S., PLEASANTS, J. M., MATTILA, H. R., SIEGFRIED, B. D. & DIVELY, G. P. (2001). Impact of Bt corn pollen on monarch butterfly populations: a risk assessment. *Proceedings of the National Academy of Sciences* **98**, 11937–11942.

*SEKAR, S. (2012). A meta−analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy?. *Journal of Animal Ecology* **81**, 174–184.

*SEMMENS, B. X., SEMMENS, D. J., THOGMARTIN, W. E., WIEDERHOLT, R., LÓPEZ–HOFFMAN, L., DIFFENDORFER, J. E., PLEASANTS, J. M., OBERHAUSER, K. S. & TAYLOR, O. R. (2016). Quasi–extinction risk and population targets for the Eastern, migratory population of monarch butterflies (*Danaus plexippus*). *Scientific Reports* **6**, 23265.

*SEMPALA, S. D. K. (1970). Observations on butterfly migration at Entebbe, Uganda. *Journal of East African Natural History* **119**, 30–34.

*SENTHILMURUGAN, B. (2005). Mukurthi National Park: A migratory route for the butterflies. *Journal of the Bombay Natural History Society* **102**, 241–242.

*SHANNON, H. J. (1926). A preliminary report on the seasonal migrations of insects. *Journal of the New York Entomological Society* **34**, 199–205.

*SHAPIRO, A. M. (1986). Seasonal phenology and possible migration of the mourning cloak butterfly Nymphalis antiopa (Lepidoptera: Nymphalidae) in California. *The Great Basin Naturalist* **46**, 112–116.

*SHAPIRO, A. M. (1982). Within–range butterfly dispersal: an urban garden as a detector. *Atala* **8**, 46–49.

*SHAPIRO, A. M. (1980a). Mediterranean climate and butterfly migration: an overview of the California fauna. *Atalanta* **11**, 181–188.

*SHAPIRO, A. M. (1980b). Evidence for a return migration of *Vanessa cardui* in northern California (Lepidoptera: Nymphalidae). *Pan Pacific Entomologist* **56**, 319–322.

*SHAPIRO, A. M. (1976). Why do California tortoiseshells migrate? *The Journal of Research on the Lepidoptera* **14**, 93–97.

* SHAPIRO, A. M. (1974). Altitudinal migration of central California butterflies. *Journal of Research on the Lepidoptera* **13**, 157–161.

*SHAPIRO, A. M. (1973). Altitudinal migration of butterflies in the central Sierra Nevada. *The Journal of Research on the Lepidoptera* **12**, 231–235.

*SHAPIRO, A. M. (1971). Range Extension for the European Skipper, *Thymelicus lineola*, in the Northeast (Lepidoptera: Hesperiidae). *Journal of the New York Entomological Society* **79**, 27–30.

*SHAPIRO, A. M. (1970). Butterfly migrations on Staten Island. *Proceedings of the Staten Island* **26**,15–19.

*SHAW, A. K. & COUZIN, I. D. (2013). Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist* **181**, 114–124.

*SIEWERT, R. R., ISERHARD, C. A., ROMANOWSKI, H. P., CALLAGHAN, C. J. & MOSER, A. (2014). Distribution patterns of riodinid butterflies (Lepidoptera: Riodinidae) from southern Brazil. *Zoological Studies* **53**, 1–10.

*SIMON, M. J. & MILLER, L. D. (1986). Observations of the butterflies of Great Inagua Island, Bahamas, with records of three species new to the island. *Bulletin of the Allyn Museum* **105**, 1–15.

*SIMPSON, S. J. & SWORD, G. A. (2010). Evolving migration. *Proceedings of the National Academy of Sciences* **107**, 16753–16754.

*SKOPHAMMER, S. *The Population Dynamics and Migration Patterns of Alpine Butterfly Colias behrii*. Alpine Butterfly Migration, 14 pp.

*SLAGER, B. H. & MALCOLM, S. B. (2015). Evidence for partial migration in the southern monarch butterfly, *Danaus erippus*, in Bolivia and Argentina. *Biotropica* **47**, 355–362.

*SMITH, D. A. & OWEN, D. F. (1997). Colour genes as markers for migratory activity: The butterfly *Danaus chrysippus* in Africa. *Oikos* **78**, 127–135.

*SMITH, D. A. (1998). Non–Mendelian segregation and variable penetrance of colour genes in the polymorphic butterfly *Danaus chrysippus* (L.). *Heredity* **80**, 474–480.

*SMITH, D. A. (2014). *African queens and their kin: a Darwinian odyssey*. Brambleby Books, 812 pp.

*SMITH, D. A., LUSHAI, G. & ALLEN, J. A. (2005). A classification of *Danaus* butterflies (Lepidoptera: Nymphalidae) based upon data from morphology and DNA. *Zoological Journal of the Linnean Society* **144**, 191–212.

*SMITH, D. A., OWEN, D. F., GORDON, I. J. & OWINY, A. M. (1993). Polymorphism and evolution in the butterfly *Danaus chrysippus* (L.) (Lepidoptera: Danainae). *Heredity*, **71**, 242–251.

*SMITH, D. S., MILLER, L. D. & MCKENZIE, F. (1991). The butterflies of Anegada, British Virgin Islands, with descriptions of a new *Calisto* (Satyridae) and a new Copaeodes (Hesperiidae) endemic to the island. *Bulletin of the Allyn Museum* **133**, 1–26.

*SMITH, D. S., RAMOS, S. J., MCKENZIE, F., MUNROE, E. & MILLER, L. D. (1988). Biogeographical affinities of the butterflies of a forgotten island: Mona (Puerto Rico). *Bulletin of the Allyn Museum* **121**, 1–36.

*SMITHERS, C. N. (1985). Migration records in Australia: 5 Lycaenidae and Nymphalinae (Lepidoptera). *The Australian Entomologist* **11**, 91–97.

*SMITHERS, C. N. (1983a). Migration records in Australia. 3. Danainae and Acraeinae (Lepidoptera: Nymphalidae). *The Australian Entomologist* **10**, 21–27.

*SMITHERS, C. N. (1983b). Migration records in Australia, 4. Pieridae (Lepidoptera) other than'Anaphaeis java teutonia'(F.). *The Australian Entomologist* **10**, 47–54.

*SMITHERS, C. N. (1978). Migration records in Australia. 2. Hesperiidae and Papilionidae (Lepidoptera). *The Australian Entomologist* **5**, 11–14.

*SMITHERS, C. N & PETERS, J. V. (1966). A Migration of *Vanessa Kershawi* (Mccoy) (Lepidoptera: Nymphalidae) in Australia. *Australian Journal of Entomology* **5**, 67–69.

*SOLENSKY, M. J. (2004). Overview of monarch migration. In *The monarch butterfly: biology and conservation* (eds K. S. Oberhauser & M. J. Solensky), Cornell University Press, pp. 79–83.

SOMVEILLE, M., MANICA, A., BUTCHART, S. H. & RODRIGUES, A. S. (2013). Mapping global diversity patterns for migratory birds. *PLoS One* **8**, e70907.

*SOUTHWOOD, T. R. E. (1981). Ecological aspects of insect migration. *Animal migration* **479**, 197–208.

*SOUTHWOOD, T. R. E. (1962). Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* **37**, 171–211.

*SPARKS, T. H., ROY, D. B. & DENNIS, R. L. H. (2005). The influence of temperature on migration of Lepidoptera into Britain. *Global Change Biology* **11**, 507–514.

*SPIETH, H. R. & CORDES, R. (2012). Geographic comparison of seasonal migration events of the large white butterfly, *Pieris brassicae*. *Ecological Entomology* **37**, 439–445.

*SPIETH, H. R., CORDES, R. G. & DORKA, M. (1998). Flight directions in the migratory butterfly *Pieris brassicae*: results from semi−natural experiments. *Ethology* **104**, 339–352.

*SPIETH, H. R. & KASCHUBA–HOLTGRAVE, A. (1996). A new experimental approach to investigate migration in *Pieris brassicae* L. *Ecological Entomology* **21**, 289–294.

*SPRANDEL, G. L. (2001). Fall dragonfly (Odonata) and butterfly (lepidoptera) migration at St. Joseph Peninsula, Gulf County, Florida. *Florida Entomologist* **84**, 234–238.

*SRYGLEY, R. B., DUDLEY, R., OLIVEIRA, E. G. & RIVEROS, A. J. (2014). El Niño, host plant growth, and migratory butterfly abundance in a changing climate. *Biotropica* **46**, 90–97.

*SRYGLEY, R. B., DUDLEY, R., OLIVEIRA, E. G., AIZPRUA, R., PELAEZ, N. Z. & RIVEROS, A. J. (2010). El Niño and dry season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical wet to dry forests. *Global Change Biology* **16**, 936–945.

*SRYGLEY, R. B. & DUDLEY, R. (2008). Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences. *Integrative and Comparative Biology* **48**, 119–133.

*SRYGLEY, R. B., DUDLEY, R., OLIVEIRA, E. G. & RIVEROS, A. J. (2006). Experimental evidence for a magnetic sense in Neotropical migrating butterflies (Lepidoptera: Pieridae). *Animal Behaviour* **71**, 183–191.

*STALLEICKEN, J., MUKHIDA, M., LABHART, T., WEHNER, R., FROST, B. & MOURITSEN, H. (2005). Do monarch butterflies use polarized skylight for migratory orientation?. *Journal of Experimental Biology* **208**, 2399–2408.

*SRYGLEY, R. B. (2001). Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Animal Behaviour* **61**, 191–203.

*SRYGLEY, R. B. & OLIVEIRA, E. G. (2001). Sun compass and wind drift compensation in migrating butterflies. *The Journal of Navigation* **54**, 405–417.

*STEFANESCU, C., PUIG−MONTSERRAT, X., SAMRAOUI, B., IZQUIERDO, R., UBACH, A. & ARRIZABALAGA, A. (2017). Back to Africa: autumn migration of the painted lady butterfly *Vanessa cardui* is timed to coincide with an increase in resource availability. *Ecological Entomology* **42**, 737–747.

*STEFANESCU, C., PÁRAMO, F., ÅKESSON, S., ALARCÓN, M., ÁVILA, A., BRERETON, T., CARNICER, J., CASSAR, L. F., FOX, R., HELIÖLÄ, J. & HILL, J. K. (2013). Multi–generational long–distance migration of insects: studying the painted lady butterfly in the Western Palaearctic. *Ecography* **36**, 474–486.

*STEFANESCU, C., SOTO, D. X., TALAVERA, G., VILA, R. & HOBSON, K. A. (2016). Long–distance autumn migration across the Sahara by painted lady butterflies: exploiting resource pulses in the tropical savannah. *Biology Letters* **12**, 20160561.

*STEFANESCU, C. (2011). Moroccan source areas of the Painted Lady butterfly *Vanessa cardui* (Nymphalidae: Nymphalinae) migrating into Europe in spring. *The Journal of the Lepidopterists' Society* **65**, 15–26.

*STEFANESCU, C., ASKEW, R. R., CORBERA, J. & SHAW, M. R. (2012). Parasitism and migration in southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). *European Journal of Entomology* **109**, 85–94.

*STEFANESCU, C., ALARCÓN, M. & ÀVILA, A. (2007). Migration of the painted lady butterfly, *Vanessa cardui*, to north–eastern Spain is aided by African wind currents. *Journal of Animal Ecology* **76**, 888–898.

*STEFANESCU, C. (2001). The nature of migration in the red admiral butterfly *Vanessa atalanta*: evidence from the population ecology in its southern range. *Ecological Entomology* **26**, 525–536.

*STEFANESCU, C. (1997). Migration patterns and feeding resources of the Painted Lady butterfly, *Cynthia cardui* (L.) (Lepidoptera, Nynphalidae) in the northeast of the Iberian peninsula. *Miscel· lània Zoològica* **20**, 31–48.

*STENOIEN, C., NAIL, K. R., ZALUCKI, J. M., PARRY, H., OBERHAUSER, K. S. & ZALUCKI, M. P. (2016). Monarchs in decline: a collateral landscape−level effect of modern agriculture. *Insect Science* **25**, 528–541.

*STEVENS, V. M., TROCHET, A., VAN DYCK, H., CLOBERT, J. & BAGUETTE, M. (2012). How is dispersal integrated in life histories: a quantitative analysis using butterflies. *Ecology Letters* **15**, 74–86.

*STEVENS, V. M., TURLURE, C. & BAGUETTE, M. (2010). A meta−analysis of dispersal in butterflies. *Biological Reviews* **85**, 625–642.

*STINNER, R. E., BARFIELD, C. S., STIMAC, J. L. & DOHSE, L. (1983). Dispersal and movement of insect pests. *Annual Review of Entomology* **28**, 319–335.

*Stirling, F. (1923). Southern Migration of Butterflies. *Florida Entomologist* **7**, 8–9.

*STOYAN, B. Migrant Lepidoptera species in Bulgaria, 1994. *Atalanta* **27**, 127–155.

*SUETSUGU, K., MUTOH, A., KATO, S., KUNITACHI, T. & ITOH, H. (2012). Emergence of migration behavior and adaptiogenesis to environments with sensory agents: Multigenerational migration of the monarch butterfly. *Electronics and Communications in Japan* **95**, 46–55.

*SUTCLIFFE, O. L., THOMAS, C. D. & PEGGIE, D. (1997). Area–dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia* **109**, 229–234.

*SUTCLIFFE, O. L. & THOMAS, C. D. (1996a). Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* **10**, 1359–1365.

*SUTCLIFFE, O. L., THOMAS, C. D. & MOSS, D. (1996b). Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology* **65**, 85–95.

SYDEMAN, W., GARCÍA–REYES, M., SCHOEMAN, D., RYKACZEWSKI, R., THOMPSON, S., BLACK, B. & BOGRAD, S. (2014). Climate change and wind intensification in coastal upwelling ecosystems. *Science* **345**, 77–80.

*TALAVERA, G., BATAILLE, C., BENYAMINI, D., GASCOIGNE–PEES, M. & VILA, R. (2018). Round–trip across the Sahara: Afrotropical Painted Lady butterflies recolonize the Mediterranean in early spring. *Biology Letters* **14**, 20180274.

*TALAVERA, G. & VILA, R. (2017). Discovery of mass migration and breeding of the painted lady butterfly *Vanessa cardui* in the Sub–Sahara: the Europe–Africa migration revisited. *Biological Journal of the Linnean Society* **120**, 274–285.

*TENNENT, J. (1995). *Danaus chrysippus* Linnaeus, 1758; a review of records and present status in the Maghreb countries of Morocco, Algeria and Tunisia (Lepidoptera, Danaidae). *Nota Lepidopterologica* **17**, 201–216.

*THAXTER, R. (1880). Swarming of *Archippus*. *Canadian Entomologist* **12**, 38–39.

*THOGMARTIN, W. E., WIEDERHOLT, R., OBERHAUSER, K., DRUM, R. G., DIFFENDORFER, J. E., ALTIZER, S., TAYLOR, O. R., PLEASANTS, J., SEMMENS, D. & SEMMENS, B. (2017). Monarch butterfly population decline in North America: identifying the threatening processes. *Royal Society Open Science* **4**, 170760.

*THOMAS, J. (2020). *The butterflies of Britain and Ireland*. Bloomsbury Publishing, 288 pp.

*TIGERS, S., CROWS, C. & TIGERS, B. (2014). Danainae congregation in the Konkan region of Maharashtra, India. *Current Science* **106**, 514.

*TRACY, J. L., KANTOLA, T., BAUM, K. A. & COULSON, R. N. (2019). Modeling fall migration pathways and spatially identifying potential migratory hazards for the eastern monarch butterfly. *Landscape Ecology* **34**, 443–458.

*TURNER, J. R. (1971). Experiments on the demography of tropical butterflies. II. Longevity and home–range behaviour in *Heliconius erato*. *Biotropica* **3**, 21–31.

*URQUHART, F. A. & URQUHART, N. R. (1979a). Aberrant autumnal migration of the eastern population of the monarch butterfly, *Danaus p. plexippus* (Lepidoptera: Danaidae) as it relates to the occurrence of strong westerly winds. *The Canadian Entomologist* **111**, 1281–1286.

*URQUHART, F. A. & URQUHART, N. R. (1979b). Vernal migration of the monarch butterfly (*Danaus p. plexippus*, Lepidoptera: Danaidae) in North America from the overwintering site in the Neo–volcanic Plateau of Mexico. *The Canadian Entomologist* **111**, 15–18.

*URQUHART, F. A. & URQUHART, N. R. (1978). Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. *Canadian Journal of Zoology* **56**, 1759–1764.

*URQUHART, F. A. & URQUHART, N. R. (1976). Migration of butterflies along the Gulf Coast of northern Florida. *Journal of the Lepidopterists' Society* **30**, 59–61.

*URQUHART, F. A. (1964). Monarch butterfly (*Danaus plexippus*) migration studies–autumnal movement. *Proceedings of the Entomological Society of Ontario* **95**, p. 23.

*URQUHART, F. A. (1960). *The monarch butterfly*. Toronto: University of Toronto Press, 394 pp.

*URQUHART, F. A. (1941). A proposed method for marking migrant butterflies. *The Canadian Entomologist* **73**, 21–22.

*VALENTINE, P. S. (2004). The demise of mass migration of the brown awl *Badamia exclamationis* (Fabricius 1775) (Lepidoptera: Hesperiidae): a consequence of land clearing in Queensland?. *Pacific Conservation Biology* **10**, 67–69.

*VÄLIMÄKI, P. & ITÄMIES, J. (2003). Migration of the clouded Apollo butterfly *Parnassius mnemosyne* in a network of suitable habitats–effects of patch characteristics. *Ecography* **26**, 679–691.

VAN KLINK, R., BOWLER, D. E., GONGALSKY, K. B., SWENGEL, A. B., GENTILE, A. & CHASE, J. M. (2020). Meta–analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420.

VAN STRIEN, A.J., VAN SWAAY, C.A., VAN STRIEN–VAN LIEMPT, W.T., POOT, M.J. & WALLISDEVRIES, M.F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation* **234**, 116–122.

*VAN SWAAY, C., CUTTELOD, A., COLLINS, S., MAES, D., MUNGUIRA, M. L., ŠAŠIĆ, M., SETTELE, J., VEROVNIK, R., VERSTRAEL, T., WARREN, M., WIEMERS, M. &

WYNHOFF, I. (2010). *European red list of butterflies*. Luxembourg: Publications Office of the European Union, 60 pp.

*VANDER ZANDEN, H. B., CHAFFEE, C. L., GONZÁLEZ–RODRÍGUEZ, A., FLOCKHART, D. T., NORRIS, D. R. & WAYNE, M. L. (2018). Alternate migration strategies of eastern monarch butterflies revealed by stable isotopes. *Animal Migration* **5**, 74–83.

*Vaughn, C. R. (1985). Birds and insects as radar targets: a review. *Proceedings of the IEEE* **73**, 205–227.

*VERMANDEL, E. & VLIEGENTHART, A. (2014). Trekvlinders en dwaalgasten in de Benelux in 2013 (Lepidoptera). *Phegea* **42**, 82–90.

*VERVLOET, A. M. (2012). *Long–distance migration in butterflies and moths: a cross–species review*. Utrecht University, 37 pp.

*VICKERMAN, D., MICHELS, A. & BURROWES, P. A. (1999). Levels of infection of migrating monarch butterflies, *Danaus plexippus* (Lepidoptera: Nymphalidae) by the parasite *Ophryocystis elektroscirrha* (Neogregarinida: Ophryocystidae), and evidence of a new mode of spore transmission between adults. *Journal of the Kansas Entomological Society* **72**, 124–128.

*VIDAL, O. & RENDÓN–SALINAS, E. (2014). Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. *Biological Conservation* **180**, 165–175.

*VLASANEK, P., HAUCK, D. & KONVICKA, M. (2009). Adult sex ratio in the *Parnassius mnemosyne* butterfly: effects of survival, migration, and weather. *Israel Journal of Ecology & Evolution* **55**, 233–252.

*WALKER, T. J. (2001). Butterfly migrations in Florida: seasonal patterns and long–term changes. *Environmental Entomology* **30**, 1052–1060.

*WALKER, T. J. (1991). Butterfly migration from and to peninsular Florida. *Ecological Entomology* **16**, 241–252.

*WALKER, T. J. & LENCZEWSKI, B. (1989). An inexpensive portable trap for monitoring butterfly migration. *Journal of the Lepidopterists' Society* **43**, 289–298.

*WALKER, T. J. (1985a). Butterfly migration in the boundary layer. In *Migration : Mechanisms and Adaptive Significance*. Contributions in Marine Science Supplement Vol 27 (ed M. A. Rankin), University of Texas Press, pp. 704–723.

*WALKER, T. J. (1985b). Permanent traps for monitoring butterfly migration: Tests in Florida, 1979–84. *Journal of the Lepidopterists' Society* **39**, 313–320.

*WALKER, T. J. (1980). Migrating Lepidoptera: are butterflies better than moths?. *The Florida Entomologist* **63**, 79–98.

*WALKER, T. J. (1978). Migration and re–migration of butterflies through north peninsular Florida: quantification with Malaise traps. *Journal of the Lepidopterists' Society* **32**, 178–190.

WALTHER, G.–R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J., FROMENTIN, J.–M., HOEGH–GULDBERG, O. & BAIRLEIN, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395.

*WALTON, R. K., BROWER, L. P. & DAVIS, A. K. (2005). Long–term monitoring and fall migration patterns of the Monarch butterfly in Cape May, New Jersey. *Annals of the Entomological Society of America* **98**, 682–689.

*WANG, H. Y. & EMMEL, T. C. (1990). Migration and overwintering aggregations of nine danaine butterfly species in Taiwan (Nymphalidae). *Journal of the Lepidopterists' Society* **44**, 216–228.

*WARREN, M. S. (1987). The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. *Journal of Applied Ecology* **24**, 483–498.

*WASSENAAR, L. I. & HOBSON, K. A. (1998). Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences* **95**, 15436–15439.

*WEHNER, R. (1984). Astronavigation in insects. *Annual Review of Entomology* **29**, 277–298.

*Wigglesworth, V. B. (1982). Carrington Bonsor Williams, 7 October 1889–12 July 1981. *Biographical Memoirs of Fellows of the Royal Society* **28**, 666–684.

*WILCOVE, D. S. (2008). Animal migration: an endangered phenomenon?. *Issues in Science and Technology* **24**, 71–78.

*WILCOVE, D. S. & WIKELSKI, M. (2008). Going, going, gone: is animal migration disappearing. *PLoS Biology* **6**, e188.

*WILLIAMS, C. B. (1958). *Insect migration*. The New Naturalist, Collins, London, 235 pp.

*WILLIAMS, C. B. (1957). Insect migration. *Annual Review of Entomology* **2**, 163–180.

*WILLIAMS, C. B., COCKBILL, G., GIBBS, M. & DOWNES, J. (1942). Studies in the migration of Lepidoptera. *Transactions of the Royal Entomological Society of London* **92**, 101–174.

*WILLIAMS, C. B. (1939a). Records of butterfly migration in Africa (Lepidopt.). *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* **14**, 69–74).

*WILLIAMS, C. B. (1939b). Some butterfly migrations in Europe, Asia and Australia. In *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* **14**, 131–137.

*WILLIAMS, C. B. (1939c). Some records of butterfly migration in America. In *Proceedings of the Royal Entomological Society of London. Series A, General Entomology* **14**, 139–144.

*WILLIAMS, C. B. (1938). The migration of butterflies in India. *Journal of the Bombay Natural History Society* **40**, 439–457.

*WILLIAMS, C. B. (1930). *The migration of butterflies*. Edinburgh & London, Oliver & Boyd, 473 pp.

*WILLIAMS, C. B. (1927). A study of butterfly migration in south India and Ceylon, based largely on records by Messrs. J. Evershed, EE Green, JCF Fryer and W. Ormiston. *Ecological Entomology* **75**, 1–33.

*WILLIAMS, C. B. (1925). The Migrations of the Painted Lady Butterfly. *Nature* **115**, 535–537.

*WILLIAMS, C. B. (1920). Records of insect migrations in tropical America. Registros de migraciones de insectos en la América tropical. *Transactions of the Royal Entomological Society of London* **1920**, 146–165.

*WITHGOTT, J. (1999). Pollination migrates to top of conservation agenda. *Bioscience* **49**, 857–862.

*WOIWOOD, I., REYNOLDS, D. R. & THOMAS, C. D. (2001). *Insect Movement: Mechanisms and Consequences* (eds I. P. Woiwod, C. D. Thomas & D. R. Reynolds), CABI, 464 pp.

*WOLDA, H. (1988). Insect seasonality: why?. *Annual Review of Ecology and Systematics* **19**, 1–18.

*WOLFE, J. J. (1899). Migratory Butterflies in South–West Cork. *The Irish Naturalist* **8**, 218–220.

*WONG, Y., LEUNG, P., SZE, W. & WONG, K. (2004). Migration and overwintering aggregation of Danaid butterflies in Hong Kong. *Hong Kong Biodiversity* **6**, 1–7.

*WOODBURY, A. M. (1941). Animal migration: periodic–response theory. *The Auk* **58**, 463–505.

*WOODRUFF, L. B. (1919). Fall Notes on Some Alabama Butterflies. *Journal of the New York Entomological Society* **27**, 159–161.

*WOODS, W. A., WOOD, C. A. L. & STEVENSON, R. D. (2004). Detecting interindividual variation in resting metabolic rate of the painted lady butterfly *Vanessa cardu*i; Why you should not offer ladies lunch. *Integrative and Comparative Biology* **44**, 668–668.

WOTTON, K. R., GAO, B., MENZ, M. H., MORRIS, R. K., BALL, S. G., LIM, K. S., REYNOLDS, D. R., HU, G. & CHAPMAN, J. W. (2019). Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology* **29**, 2167–2173. e2165.

*WU, C. & XU, Y. (2017). *Butterflies of China*. Vol. 1–4, Straits Publishing House, 2077 pp.

*YAKUBU, A. A., SÁENZ, R., STEIN, J. & JONES, L. E. (2004). Monarch butterfly spatially discrete advection model. *Mathematical Biosciences* **190**, 183–202.

*YANG, L. H., OSTROVSKY, D., ROGERS, M. C. & WELKER, J. M. (2016). Intra−population variation in the natal origins and wing morphology of overwintering western monarch butterflies *Danaus plexippus*. *Ecography* **39**, 998–1007.

*YIU, V. (2009). Winter aggregation of Danaine Butterflies in Hong Kong (1999–2009). Ten years records and a brief account. *Hong Kong Entomological Bulletin* **1**, 38–55.

*YOUNG, L. C. H. (1914). The Distribution of Butterflies in India, *Journal of the Bombay Natural History Society* **15**, 594–601.

*Zalucki, M. P. & Clarke, A. R. (2004). Monarchs across the Pacific: the Columbus hypothesis revisited. *Biological Journal of the Linnean Society* **82**, 111–121.

*Zalucki, M. P., Brower, L. P. & Alonso−M, A. (2001). Detrimental effects of latex and cardiac glycosides on survival and growth of first−instar monarch butterfly larvae *Danaus plexippus* feeding on the sandhill milkweed *Asclepias humistrata*. *Ecological Entomology,* **26** 212–224.

*Zalucki, M. P. & Suzuki, Y. (1987). Milkweed patch quality, adult population structure, and egg laying in the monarch butterfly. *Journal of the Lepidopterists' Society* **41**, 13–22.

*Zalucki, M. & Kitching, R. (1982). Temporal and spatial variation of mortality in field populations of *Danaus plexippus* L. and *D. chrysippus* L. larvae (Lepidoptera: Nymphalidae). *Oecologia* **53**, 201–207.

*Zalucki, M. P., Kitching, R. L., Abel, D. & Pearson, J. (1980). A novel device for tracking butterflies in the field. *Annals of the Entomological Society of America*, **73**, 262–265.

*Zaya, D. N., Pearse, I. S. & Spyreas, G. (2017). Long–term trends in Midwestern milkweed abundances and their relevance to monarch butterfly declines. *BioScience*, **67**, 343–356.

*Zhan, S., Zhang, W., Niitepold, K., Hsu, J., Haeger, J. F., Zalucki, M. P., Altizer, S., de Roode, J. C., Reppert, S. M. & Kronforst, M. R. (2014). The genetics of monarch butterfly migration and warning colouration. *Nature* **514**, 317–321.

*Zhu, H., Gegear, R. J., Casselman, A., Kanginakudru, S. & Reppert, S. M. (2009). Defining behavioral and molecular differences between summer and migratory monarch butterflies. *BMC Biology* **7**, 1–14.

*ZHU, H., SAUMAN, I., YUAN, Q., CASSELMAN, A., EMERY–LE, M., EMERY, P. & REPPERT, S. M. (2008). Cryptochromes define a novel circadian clock mechanism in monarch butterflies that may underlie sun compass navigation. *PLoS Biology* **6**, e4.

*ZHU, H., CASSELMAN, A. & REPPERT, S. M. (2008). Chasing migration genes: a brain expressed sequence tag resource for summer and migratory monarch butterflies (*Danaus plexippus)*. *PLoS One* **3**, e1345.

*ZIPKIN, E. F., RIES, L., REEVES, R., REGETZ, J. & OBERHAUSER, K. S. (2012). Tracking climate impacts on the migratory monarch butterfly. *Global Change Biology* **18**, 3039–3049.