



Mass-migrating bumblebees: An overlooked phenomenon with potential far-reaching implications for bumblebee conservation

Thijs P. M. Fijen

Plant Ecology and Nature Conservation
Group, Wageningen University, Wageningen,
The Netherlands

Correspondence

Thijs P. M. Fijen
Email: thijs.fijen@wur.nl

Funding information

Nederlandse Organisatie voor
Wetenschappelijk Onderzoek, Grant/Award
Number: E10009

Handling Editor: Silke Bauer

[Correction added on 17 November 2020,
after first online publication: In Table 1, the
3rd and 4th column have been changed.]

Abstract

1. Bumblebees are one of the most commonly studied pollinators, but they are declining in large parts of their distribution. Whether bumblebees can cope with anthropogenic disturbances such as climate change and habitat loss depends largely on their dispersal capacity. While bumblebee queen dispersal is estimated to be only a few kilometres, bird migration sites have documented mass-migration events with peak migration of 70 bumblebee queens per minute, indicating that bumblebees can migrate over larger distances than previously thought.
2. The open-access database trektellen.org contains 10 daily counts of >1,000 migrating queens past single points in the Netherlands, and one in the United Kingdom (total bumblebee records 65,430; range 1–11,142 individuals), mostly in early spring. Such mass-migration events are poorly documented in the scientific literature, and usually when describing migrations of other insects such as syrphids and social wasps.
3. Most common European bumblebee species were documented to migrate. Bumblebees were observed flying at sea, coming from sea and flying towards the sea, showing that they can cross large water bodies. The wind direction might have helped to concentrate migration at landscape bottlenecks. On 1 day, bumblebee mass-migration was documented on two sites located 200 km apart. Together with the concentrated and directional flight this suggests that they can migrate for several hundreds of kilometres.
4. Because most mass-migration events occur in spring, large-scale shortage in suitable nesting sites may be the trigger for mass-migration (e.g. due to high queen survival or low vole numbers). Future studies should test whether this is the case, or whether bumblebees show annual seasonal migration.
5. *Synthesis and applications.* Much remains unclear about bumblebee migration, but it may have large consequences for the conservation of bumblebees and the ecosystem services they provide. For example, bumblebees in highly disturbed areas like agricultural landscapes may be continuously supplemented by queens from far-away productive natural areas. This suggests that large-scale conservation initiatives are required to maintain viable populations of common and endangered

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2020 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

species. Structured observations and modern-day technology, like isotope analyses or radar monitoring, may shed light on the drivers and consequences of the overlooked phenomenon of bumblebee migration.

KEYWORDS

bumblebee, colonisation, conservation, dispersal, ecosystem services, mass-migration, migration

1 | INTRODUCTION

Bumblebees *Bombus* are large and attractive bees, and as a result have received much attention from researchers with hundreds of scientific papers and several monographs having dealt with the genus (e.g. Goulson, 2010; Sladen, 1912). They are the most important native crop pollinators in Europe and North America (Kleijn et al., 2015), and are showing pronounced declines throughout these continents (Bartomeus et al., 2013; Carvalheiro et al., 2013). Habitat loss and climate change are main contributors to the declining spread of these bumblebees (Illes et al., 2018; Soroye et al., 2020). Whether bumblebees can cope with climate change and habitat loss depends largely on their dispersal capacity (Illes et al., 2018; Sirois-Delisle & Kerr, 2018), which is generally considered to be only a few kilometres (Carvell et al., 2017; Makinson et al., 2019; Mola & Williams, 2019). Yet, bird migration counting sites in Europe have documented massive migration of bumblebee queens in spring, showing that bumblebee queens can move over much larger distances than evidence suggests (Mola & Williams, 2019). The ability to move over long distances influences important ecological processes, such as genetic exchange and disease spread, and suggests that bumblebee population dynamics occur on a much larger scale than previously thought.

2 | TREKTELLEN.ORG DATABASE

There is a vast network of bird migration counting sites across north-western-Europe where observers regularly count birds on migration (Troost & Boele, 2019). Many of these counts are entered into the open-access database Trektellen.org that aims to share and document bird migration data (note: 'trek-tellen' is Dutch for 'migration'-'counting'; Trektellen.org). Each group of observers of a site determines when to count, which species (e.g. all, or only raptors) and how detailed they want the counts to be (e.g. to specify age, sex and plumage details).

3 | BUMBLEBEE MASS-MIGRATION EVENTS

Insect migration is only irregularly documented, based on the interest of observers, and the trektellen.org database contains a total of 65,430 migrating bumblebees up to 1 August 2020, of which 95% of the individuals originate from the Netherlands (Trektellen.org). The three largest bird migration counting sites in the Netherlands have registered bumblebee mass-migration events with up to 70 individuals per minute during peak migration (Mervyn Roos, ketelbrug.nl). Up to 1 August 2020, 10 Dutch counts exceed 1,000 migrating

Bumblebee sp. - average number per hour/standard week

■ ($h = 2,270,189:05/n = 65,430$)

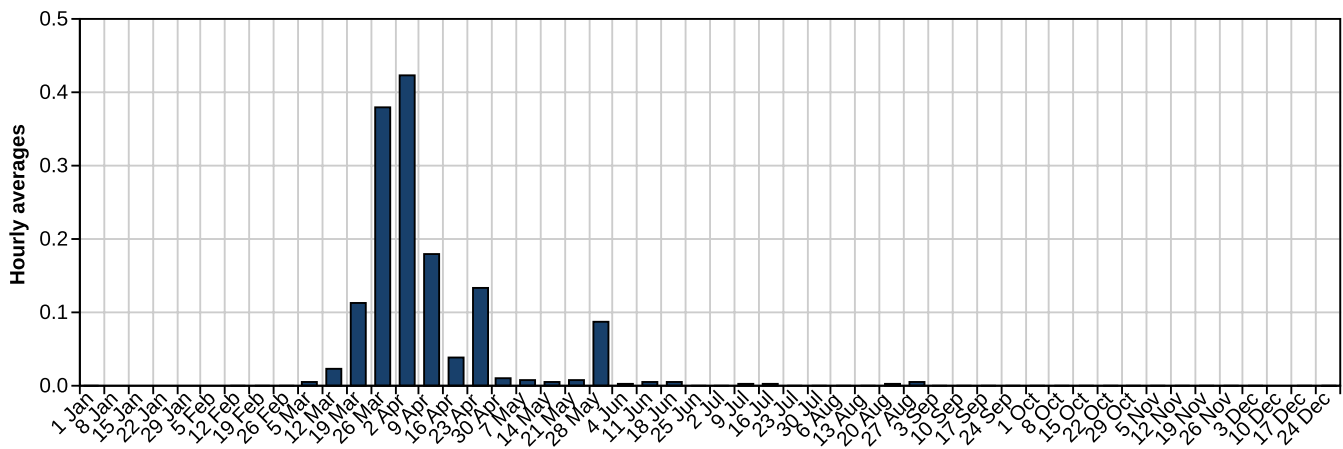


FIGURE 1 Weekly totals of bumblebee counts in the trektellen.org database on 1 August 2020. In well over 2 million hours of migration counts (indicated by 'h'), a total of 65,430 bumblebees were counted (indicated by 'n'). Source: <https://trektellen.org/species/graph/0/0/1119/>

TABLE 1 Dates and locations of published counts of bumblebee migration. Data from trektellen.org only on days with more than 1,000 individuals counted (trektellen.org)

Date	Site	Longitude (decimal)	Latitude (decimal)	Total count (individuals)	Hours observed (hh:mm)	Source
1 August 1955	Trouville (FR)	0.0818	49.3738	Few		Lane (1955)
4 September 1955	Spurn (UK)	0.1153	53.6580	1 per minute	03:20	Owen (1956)
28 May 1956	Cumbria (UK)	-3.3451	54.2198	3-4 per minute	04:00	Birkett (1956)
16-20 June 1957	Falsterbo (SE)	12.8266	55.3853	Some		Rudebeck (1965)
May-June 1975-1977	South Finland (FIN)	24.4435	59.9884	Up to 900/hr		Mikkola (1978)
22 May 1979	Baltic Sea (FIN)	24.7584	59.7761	5		Mikkola (1984)
1 April 2005	Kamperhoek (NL)	5.6413	52.6067	11,142	11:15	trektellen.org
2 April 2005	Kamperhoek (NL)	5.6413	52.6067	10,180	11:45	trektellen.org
24 April 2005	Kamperhoek (NL)	5.6413	52.6067	5,895	14:15	trektellen.org
6 April 2009	Kamperhoek (NL)	5.6413	52.6067	1,626	08:30	trektellen.org
6 April 2009	Breskens (NL)	3.5236	51.4040	2,200	13:30	trektellen.org
29 May 2009	Bradford (UK)	-1.9253	53.7969	2,000	07:00	trektellen.org
30 March 2014	Kamperhoek (NL)	5.6413	52.6067	1,738	09:30	trektellen.org
9 April 2016	Noordkaap (NL)	6.7500	53.4654	3,387	10:30	trektellen.org
12 April 2016	Eemshaven (NL)	6.7444	53.4655	1,122	11:30	trektellen.org
7 April 2018	Breskens (NL)	3.5236	51.4040	2,790	07:55	trektellen.org
24 March 2020	Breskens (NL)	3.5236	51.4040	2,512	10:42	trektellen.org

bumblebee queens on a single day, all around early April (Figure 1) in six different years (Table 1). In addition, one count in the database from the United Kingdom (Bradford) estimated 2000 queens migrating westward in the end of May ($M 4,053.8 \pm 3,345$ SD individuals; range 1,122-11,142 individuals, Table 1). In most cases individuals were counted using a tally counter, but during peak moments 1-min focussed counting was extrapolated to 15-min counts. Because bumblebee migration is not part of the standard protocol for bird migration counts, and only a small fraction of the observers documents insects on migration, it is likely that migration happens more frequently and that the actual numbers are much higher.

Such migration events are only sparsely documented in the scientific literature and are mostly just mentioned when describing movement of other migrating insects. For example, bumblebees migrated among the numbers of butterflies in northern France (Lane, 1955), together with syrphids along the Yorkshire coast in the United Kingdom (Owen, 1956), and with social wasps in Falsterbo, Sweden (Rudebeck, 1965) and southern Finland (Mikkola, 1978, 1984; Figure 2). However, Birkett (1956) mentions a migration event of about three or four bumblebees (tentatively identified as *Bombus lucorum*) passing per minute in 4 hr observing along the Cumbria coast (United Kingdom) without other insects obviously migrating. Also none of the 1,000+ counts in the Netherlands mentioned substantial migration of other insects (e.g. painted lady migration; Stefanescu et al., 2013), even though butterflies are more regularly documented in the database. The few publications mentioning bumblebee migration are in stark contrast with the total number of bumblebee publications, which suggests that bumblebee mass-migration is largely overlooked.

There is more or less consensus that these directional mass movements of insects can be called migration (Holland et al., 2006). While for 'true' migration (e.g. in birds and mammals) single individuals should be travelling back and forth, this has never been documented for insects. Migrating insects generally track the season, and their offspring travels in reversed direction (Chapman et al., 2015). This poses the question whether bumblebee queens (and males) migrate in autumn as well. Migration events in mid-June at Falsterbo (Rudebeck, 1965), and in September along the Yorkshire coast in the United Kingdom (Owen, 1956) indicate that this indeed may be the case, but observations are rare in the trektellen.org database (Figure 1), despite the large interest in autumnal bird migration. Whether bumblebees migrate southwards in autumn needs to be validated by more structured counting.

4 | BUMBLEBEE MIGRANTS ARE NOT DETERRED BY LARGE WATER BODIES

Strikingly, most documented mass-migration events have in common that they occur near coastlines at well-known bird migration bottlenecks close to large water bodies, or at sea (Figure 2), suggesting that when bumblebees encounter large water bodies they often follow the shore but may also decide to cross the sea to continue their journey (Figure 3). Bumblebees were even observed on light ships at sea (Heydemann, 1967), flying at sea at about 50 km from the coast (Mikkola, 1984), coming from the sea (Lane, 1955) or flying from the coast towards the sea (Rudebeck, 1965). This behaviour could explain

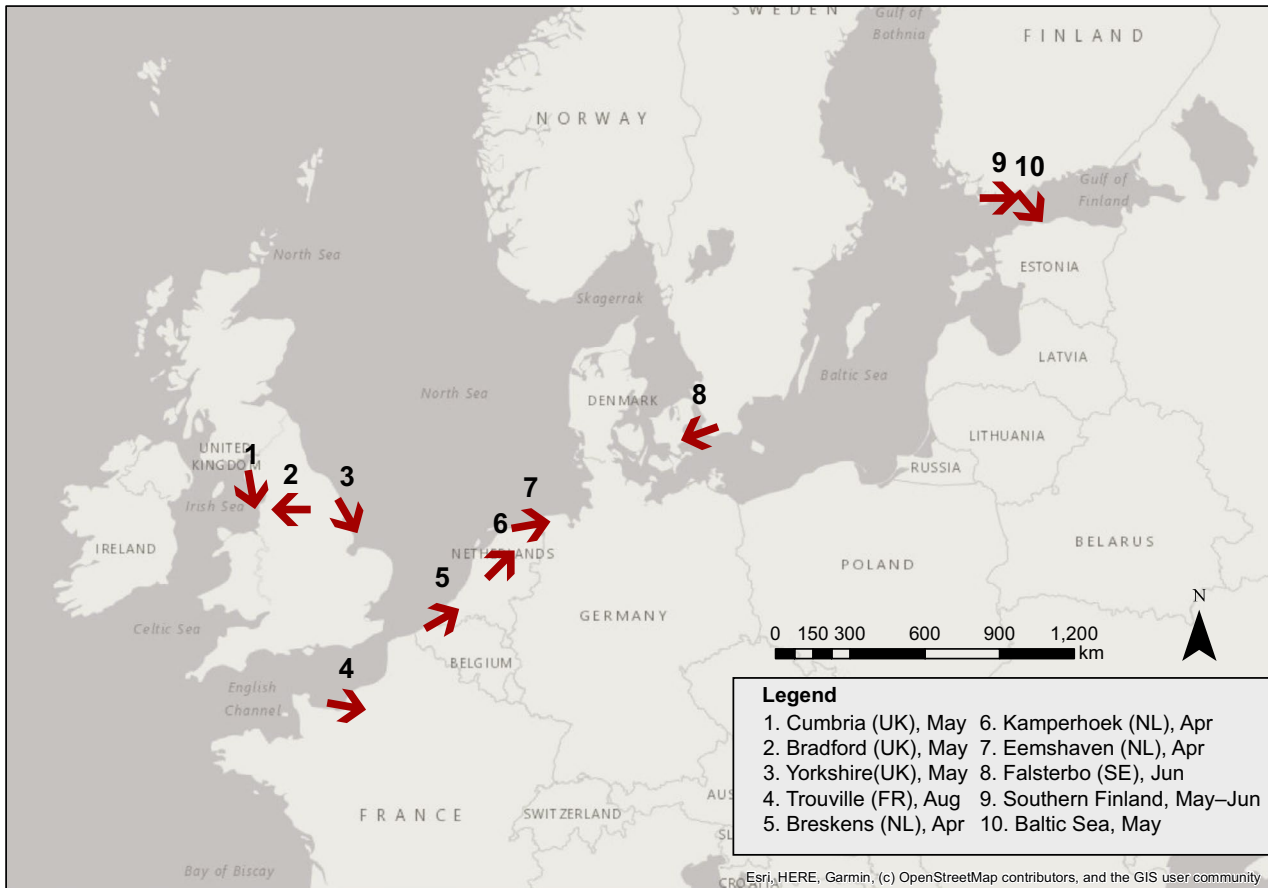


FIGURE 2 Locations of documented bumblebee migration events in north-western-Europe. Data from trektellen.org only on days with more than 1,000 individuals counted. The arrows indicate the dominant flight direction



FIGURE 3 Bumblebees on migration at the Noordkaap, the Netherlands on 9 April 2016. A total of 3,387 queens were arrived from the Wadden Sea from the north, and then turned to follow the sea dike eastwards (picture by Jacob Bosma)

the recent colonisation of Iceland by several continental bumblebee species (Potapov et al., 2018). While bumblebees migrating over sea may have stumbled upon Iceland before, the current, warmer climate may have allowed populations to establish only recently.

5 | THE INFLUENCE OF WEATHER ON BUMBLEBEE MIGRATION

The weather circumstances seem to play an important role in documenting these mass-migration events. Most scientific publications describe how the weather conditions seemed to be favourable for insect migration (e.g. Mikkola, 1978), and the described weather conditions during the Dutch counts support this. Weather was generally fine, relatively warm and sunny for the time of the year and with a gentle breeze. In most locations, the wind direction has helped to 'push' the bumblebees towards the coastline (e.g. Rudebeck, 1965), concentrating the stream of insects. This is a well-known phenomenon for migration (hence the choice of location for bird migration counts at these bottlenecks). It does, however, beg the question whether bumblebee mass-migration events are dependent on these circumstances, or whether migration occurs nevertheless, albeit less concentrated.

6 | WHICH SPECIES SHOW MIGRATORY BEHAVIOUR?

While species identification on the wing is not easy, many of the common European bumblebee species were recorded in these

migration events. Species from the white-tailed species complex (queens of this complex are not identifiable on the wing; c.f. (Carolan et al., 2012; Williams et al., 2012) such as *Bombus terrestris*, *B. lucorum* and *Bombus ruderatus* were observed most frequently (remarks in Birkett, 1956; Lane, 1955; Mikkola, 1978; trektellen.org), followed in frequency by the somewhat later migrating *Bombus lapidarius* (Heydemann, 1967; Mikkola, 1978). *Bombus hypnorum* was occasionally recorded (Mikkola, 1978; Trektellen.org), and this fits with the finding based on molecular data that *B. hypnorum* has colonised the United Kingdom in recent decades (Goulson & Williams, 2001) following continuous immigration from mainland Europe (Crowther, 2017). Also the less abundant species such as *Bombus pratorum* and *Bombus pascuorum* are occasionally observed (Mikkola, 1978; Trektellen.org). This suggests that many of the bumblebee species can show migratory behaviour. However, bumblebee migration has mostly been documented in Europe, except for a single record of two unknown bumblebee species across a Nepalese mountain pass (Gatter, 1980), and the invasion reports of European species in non-native areas (e.g. Schmid-Hempel et al., 2014). It would be interesting to study whether North American and Asian species show migratory behaviour as well.

7 | THE SCALE OF BUMBLEBEE MIGRATION

The concentrated directional movement, combined with the numbers of individuals counted, indicate that bumblebee migration happens on a large scale, and that they travel considerable distances. Remarkably, two sites located 200 km apart in the Netherlands recorded mass-migration events on the same day (Table 1), demonstrating that bumblebee migration occurs on a large front. The flight speed of migrating bumblebees in Finland was estimated to be about 30 km/hr (Mikkola, 1978), and when offered nectar (flowering *Salix* sp.), some queens only landed very shortly and continued migration (Mikkola, 1984). Given that bumblebees were passing these observation points for several hours (up to 8 hr a day), it is possible that individuals migrate several hundreds of kilometres, occasionally stopping to refuel. Further indications of the distances bumblebees may travel can be found in areas where white-tailed bumblebees *B. terrestris* were introduced. For example, introduced white-tailed bumblebees *B. terrestris* in Chile have extended their distribution with an impressive 200 km per year (Schmid-Hempel et al., 2014), and with 140 km per year in New Zealand (Hopkins, 1914). In other areas this rate is lower (Hingston et al., 2002; Kadoya & Washitani, 2010; Torretta et al., 2006), but on average still a lot more than the measured dispersal rate of a few kilometres in queen dispersal studies (Mola & Williams, 2019). This gives good hope for bumblebee conservation, because it suggests that if the habitat is suitable, bumblebees can (re-)colonise it rapidly from close-by and from far-away locations.

8 | WHY DO BUMBLEBEES MIGRATE? AND WHERE DO THEY GO?

Like in other migrating insects, several hypotheses can be thought of to explain why bumblebees migrate, for example, to avoid extreme temperatures, to lower disease pressure, to escape parasites and enemies or to track resources such as food and nesting sites (Chapman et al., 2015; Winger et al., 2019). That (most) mass-migration events occur in spring suggests that a shortage of suitable nesting sites at the place of origin could be the driver of the events. Suitable nesting sites are a critical resource for bumblebee queens, and queens regularly fight for life or death over nest sites (Sladen, 1912). Severe competition for nesting sites may, for example, arise after years of low vole numbers (Vepsäläinen & Savolainen, 2000), of which the abandoned nests are often used by bumblebees, or in years with large numbers of surviving hibernating queens due to a short winter (Beekman et al., 1998). Volecycli and short winters usually occur on large spatial scales, which could then trigger mass-migration in search of areas with less competition for nest sites. As these situations do not occur yearly, this could explain why mass-migration is more apparent in some years than others.

The general trend in direction of the migration is that the bumblebees track the season and move north(-east)wards in spring on the Northern Hemisphere. However, the counts along the Cumbria coast (Birkett, 1956) and Falsterbo (Rudebeck, 1965) stand out for being in opposite direction. Instead of tracking the seasons (i.e. moving north(-east)wards), these bumblebees may have been moving away from highly productive areas (in terms of survival of wintering queens) in search of suitable nesting sites (i.e. 'nesting site limitation'). In the case of the event at Falsterbo, the alternative hypothesis could be that these were newly hatched queens from the first generation showing reversed (autumnal) migration (i.e. 'seasonal migration'). Whether nesting site limitation or seasonal migration (i.e. avoiding long and cold winters), or perhaps both, drive bumblebee migration are exciting hypotheses to test in future studies.

9 | IMPLICATIONS FOR BUMBLEBEE CONSERVATION

Bumblebee migration has far-reaching implications on the way we think about bumblebee conservation and the ecosystem services they provide. As an example: bumblebees from the white-tailed group and red-tailed bumblebees are dominant wild crop pollinators throughout Europe (Kleijn et al., 2015) and seem to be able to persist in even the most intensively farmed landscapes (Redhead et al., 2018). The current explanation for their persistence in these landscapes is based on the assumption that what little is left of the semi-natural habitats is sufficient to sustain viable populations. However, the alternative explanation based on these mass-migration events is that these populations persist because they are

continuously supplemented with bumblebees from highly reproductive natural areas (Persson & Smith, 2013) that are located far away. Effects of long-distance migration on provision of pollination services in agricultural landscapes should therefore be explored, for example by incorporating it into models predicting the ecosystem service delivery (Becher et al., 2018; Lonsdorf et al., 2009), to find out to what extent local service provision depends on distantly located natural areas.

Bumblebee migration can also play an important role in source-sink dynamics of endangered bumblebees (Iles et al., 2018). Future studies should assess the role of mass-migration in the genetic exchange between populations of these species (Ellis et al., 2006). These studies could suggest that in addition to local conservation efforts in areas where species are most endangered, large-scale conservation programs, such as National Pollinator Strategies (Defra, 2014), are required to maintain viable (source) populations of bumblebee species.

Even though bumblebees are well-researched, they still have many secrets for us to discover. We now need structural bumblebee migration counts to reveal the exact extent of this phenomenon, and the use of modern technologies like isotope analyses (Hallworth et al., 2018), genetic analyses (Carvell et al., 2017) and radar monitoring (Makinson et al., 2019; Wotton et al., 2019) may help us to do so.

ACKNOWLEDGEMENTS

T.P.M.F. acknowledges funding from 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND program, and the funding organisation NWO under grant number E10009. The author thanks the volunteers who counted bumblebees, Gerard Troost for making the data easily accessible, Mervyn Roos for discussing the topic, Jacob Bosma for providing the picture, Ivo Roessink for granting access at Sinderhoeve, and David Kleijn and Jasper van Ruijven for providing comments on earlier drafts of this paper.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.djh9w0vvr> (Fijen, 2020) and is continuously updated on trekrellen.org.

ORCID

Thijs P. M. Fijen  <https://orcid.org/0000-0002-4371-2708>

REFERENCES

- Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., Hedtke, S. M., & Winfree, R. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 4656–4660. <https://doi.org/10.1073/pnas.1218503110>
- Becher, M. A., Twiston-Davies, G., Penny, T. D., Goulson, D., Rotheray, E. L., & Osborne, J. L. (2018). Bumble-BEEHAVE: A systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. *Journal of Applied Ecology*, *55*, 2790–2801. <https://doi.org/10.1111/1365-2664.13165>
- Beekman, M., Stratum, P., & Lingeman, R. (1998). Diapause survival and post-diapause performance in bumblebee queens (*Bombus terrestris*). *Entomologia Experimentalis et Applicata*, *89*, 207–214. <https://doi.org/10.1046/j.1570-7458.1998.00401.x>
- Birkett, N. (1956). Some observations on a flight of *Bombus lucorum*. L.(Hym., Bombidae). *The Entomologist's Monthly Magazine*, *92*, 333.
- Carolan, J. C., Murray, T. E., Fitzpatrick, Ú., Crossley, J., Schmidt, H., Cederberg, B., McNally, L., Paxton, R. J., Williams, P. H., & Brown, M. J. F. (2012). Colour patterns do not diagnose species: Quantitative evaluation of a DNA barcoded cryptic bumblebee complex. *PLoS ONE*, *7*, e29251. <https://doi.org/10.1371/journal.pone.0029251>
- Carvalho, L. G., Kunin, W. E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W. N., Fox, R., Groom, Q., Hennekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Miché, D., Rasmont, P., Ode, B., Potts, S. G., Reemer, M., Roberts, S. P. M., Schaminée, J., WallisDeVries, M. F., & Biesmeijer, J. C. (2013). Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, *16*, 870–878. <https://doi.org/10.1111/ele.12121>
- Carvell, C., Bourke, A. F. G., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., Redhead, J. W., Sumner, S., Wang, J., & Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*, 547–549. <https://doi.org/10.1038/nature21709>
- 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. <https://doi.org/10.1111/ele.12407>
- Crowther, L. (2017). *The Tree Bumblebee, Bombus hypnorum: Ecology and genetics of a naturally colonising pollinator*. University of East Anglia.
- Defra. (2014). *The National Pollinator Strategy: For bees and other pollinators in England*. The Department for Environment, Food and Rural Affairs
- Ellis, J., Knight, M. E., Darvill, B., & Goulson, D. (2006). Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera: Apidae). *Molecular Ecology*, *15*, 4375–4386. <https://doi.org/10.1111/j.1365-294X.2006.03121.x>
- Fijen, T. P. M. (2020). Data from: Mass-migrating bumblebees: An overlooked phenomenon with potential far-reaching implications for bumblebee conservation. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.djh9w0vvr>
- Gatter, W. (1980). Nordwärts gerichtete Frühjahrswanderungen paläarktischer Schmetterlinge, Fliegen und Hummeln im Himalaya- und Transhimalayagebiet Nepals. *Atalanta*, *11*, 188–196.
- Goulson, D. (2010). *Bumblebees: Behaviour, ecology, and conservation* (2nd ed.). Oxford University Press.
- Goulson, D., & Williams, P. (2001). *Bombus hypnorum* (L.) (Hymenoptera: Apidae), a new British bumblebee? *British Journal of Entomology and Natural History*, *14*, 129–131.
- Hallworth, M. T., Marra, P. P., McFarland, K. P., Zahendra, S., & Studds, C. E. (2018). Tracking dragons: Stable isotopes reveal the annual cycle of a long-distance migratory insect. *Biology Letters*, *14*, 20180741. <https://doi.org/10.1098/rsbl.2018.0741>
- Heydemann, B. (1967). Der Überflug von Insekten über Nord- und Ostsee nach Untersuchungen auf Feuerschiffen. *Deutsche Entomologische Zeitschrift*, *14*, 185–215. <https://doi.org/10.1002/mmnd.19670140114>
- Hingston, A. B., Marsden-smedley, J., Driscoll, D. A., Corbett, S., Fenton, J., Anderson, R., Plowman, C., Mowling, F., Jenkin, M., Matsui, K., Bonham, K. J., Iłowski, M., Mcquillan, P. B., Yaxley, B., Reid, T., Storey, D., Poole, L., Mallick, S. A., Fitzgerald, N., ... Desmarchelier, J. M. (2002). Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecology*, *27*, 162–172. <https://doi.org/10.1046/j.1442-9993.2002.01179.x>
- Holland, R. A., Wikelski, M., & Wilcove, D. S. (2006). How and why do insects migrate? *Science*, *313*, 794–796. <https://doi.org/10.1126/science.1127272>

- Hopkins, I. (1914). History of the bumblebee in New Zealand: Its introduction and results. *NZ Department of Agriculture Bulletin*, 46, 1–29.
- Iles, D. T., Williams, N. M., Crone, E. E., & Beggs, J. (2018). Source-sink dynamics of bumblebees in rapidly changing landscapes. *Journal of Applied Ecology*, 55, 2802–2811. <https://doi.org/10.1111/1365-2664.13175>
- Kadoya, T., & Washitani, I. (2010). Predicting the rate of range expansion of an invasive alien bumblebee (*Bombus terrestris*) using a stochastic spatio-temporal model. *Biological Conservation*, 143, 1228–1235. <https://doi.org/10.1016/j.biocon.2010.02.030>
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L. K., Rader, R., Ricketts, T. H., Williams, N. M., Lee Adamson, N., Ascher, J. S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J. C., Blitzer, E. J., ... Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6, 7414. <https://doi.org/10.1038/ncomms8414>
- Lane, C. (1955). Insect migration on the north coast of France. *Entomologist's Monthly Magazine*, 91, 301–306.
- Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, 103, 1589–1600. <https://doi.org/10.1093/aob/mcp069>
- Makinson, J. C., Woodgate, J. L., Reynolds, A., Capaldi, E. A., Perry, C. J., & Chittka, L. (2019). Harmonic radar tracking reveals random dispersal pattern of bumblebee (*Bombus terrestris*) queens after hibernation. *Scientific Reports*, 9, 4651. <https://doi.org/10.1038/s41598-019-40355-6>
- Mikkola, K. (1978). Spring migrations of wasps and bumble bees on the southern coast of Finland (Hymenoptera: Vespidae and Apidae). *Annales Entomologici Fennici*, 44, 10–26.
- Mikkola, K. (1984). Spring migrations of wasp and bumblebee queens across the Gulf of Finland (Hymenoptera: Vespidae and Apidae). *Notulae Entomologicae*, 64, 125–128.
- Mola, J. M., & Williams, N. M. (2019). A review of methods for the study of bumble bee movement. *Apidologie*, 50, 497–514. <https://doi.org/10.1007/s13592-019-00662-3>
- Owen, D. (1956). A migration of insects at Spurn Point, Yorkshire. *Entomologist's Monthly Magazine*, 92, 43–44.
- Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, Ecosystems & Environment*, 165, 201–209. <https://doi.org/10.1016/j.agee.2012.12.008>
- Potapov, G. S., Kondakov, A. V., Kolosova, Y. S., Tomilova, A. A., Filippov, B. Y., Gofarov, M. Y., & Bolotov, I. N. (2018). Widespread continental mtDNA lineages prevail in the bumblebee fauna of Iceland. *ZooKeys*, 774, 141–153. <https://doi.org/10.3897/zookeys.774.26466>
- Redhead, J. W., Woodcock, B. A., Pocock, M. J. O., Pywell, R. F., Vanbergen, A. J., & Oliver, T. H. (2018). Potential landscape-scale pollinator networks across Great Britain: Structure, stability and influence of agricultural land cover. *Ecology Letters*, 21, 1821–1832. <https://doi.org/10.1111/ele.13157>
- Rudebeck, G. (1965). On a migratory movement of wasps, mainly *Vespula rufa* (L.), at Falsterbo, Sweden. *Proceedings of the Royal Entomological Society of London. Series A, General Entomology*, 40, 1–8.
- Schmid-Hempel, R., Eckhardt, M., Goulson, D., Heinzmann, D., Lange, C., Plischuk, S., Escudero, L. R., Salathé, R., Scriven, J. J., & Schmid-Hempel, P. (2014). The invasion of southern South America by imported bumblebees and associated parasites. *Journal of Animal Ecology*, 83, 823–837. <https://doi.org/10.1111/1365-2656.12185>
- Sirois-Delisle, C., & Kerr, J. T. (2018). Climate change-driven range losses among bumblebee species are poised to accelerate. *Scientific Reports*, 8, 14464. <https://doi.org/10.1038/s41598-018-32665-y>
- Sladen, F. W. L. (1912). *The humble-bee*. Cambridge University Press. <https://doi.org/10.1017/cbo9781107705739>
- Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, 367, 685–688. <https://doi.org/10.1126/science.aax8591>
- Stefanescu, C., Páramo, F., Åkesson, S., Alarcón, M., Ávila, A., Brereton, T., Carnicer, J., Cassar, L. F., Fox, R., Heliölä, J., Hill, J. K., Hirneisen, N., Kjellén, N., Kühn, E., Kuussaari, M., Leskinen, M., Liechti, F., Musche, M., Regan, E. C., ... Chapman, J. W. (2013). Multi-generational long-distance migration of insects: Studying the painted lady butterfly in the Western Palaearctic. *Ecography*, 36, 474–486. <https://doi.org/10.1111/j.1600-0587.2012.07738.x>
- Torretta, J. P., Medan, D., & Abrahamovich, A. H. (2006). First record of the invasive bumblebee *Bombus terrestris* (L.) (Hymenoptera, Apidae) in Argentina. *Transactions of the American Entomological Society*, 132, 285–289. <https://doi.org/10.17161/jom.v0i71.6520>
- Trektellen.org. Retrieved from <https://trektellen.nl/species/records/1/0/1119/0/0?language=english>
- Troost, G., & Boele, A. (2019). Trektellen.org – Store, share and compare migration data. *Bird Census News*, 32, 17–26.
- Vepsäläinen, K., & Savolainen, R. (2000). Are spring mass migrations of bumblebees and wasps driven by vole cyclicity? *Oikos*, 91, 401–404. <https://doi.org/10.1034/j.1600-0706.2000.910221.x>
- Williams, P. H., Brown, M. J. F., Carolan, J. C., An, J., Goulson, D., Aytekin, A. M., Best, L. R., Byvaltsev, A. M., Cederberg, B., Dawson, R., & Xie, Z. (2012). Unveiling cryptic species of the bumblebee subgenus *Bombus* s. str. worldwide with COI barcodes (Hymenoptera: Apidae). *Systematics and Biodiversity*, 10, 21–56. <https://doi.org/10.1080/14772000.2012.664574>
- Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2019). A long winter for the Red Queen: Rethinking the evolution of seasonal migration. *Biological Reviews of the Cambridge Philosophical Society*, 94, 737–752. <https://doi.org/10.1111/brv.12476>
- Wotton, K. R., Gao, B., Menz, M. H. M., Morris, R. K. A., 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(13), 2167–2173.e5. <https://doi.org/10.1016/j.cub.2019.05.036>

How to cite this article: Fijen TPM. Mass-migrating bumblebees: An overlooked phenomenon with potential far-reaching implications for bumblebee conservation. *J Appl Ecol*. 2020;00:1–7. <https://doi.org/10.1111/1365-2664.13768>