

ECOGRAPHY

Review and synthesis

Environmental effects on flying migrants revealed by radar

Paolo Becciu, Myles H. M. Menz, Annika Aurbach, Sergio A. Cabrera-Cruz, Charlotte E. Wainwright, Martina Scacco, Michał Ciach, Lars B. Pettersson, Ivan Maggini, Gonzalo M. Arroyo, Jeffrey J. Buler, Don R. Reynolds and Nir Sapir

P. Becciu (<http://orcid.org/0000-0002-5619-9747>) ✉ (pbecciu89@gmail.com) and N. Sapir, Animal Flight Laboratory, Dept of Evolutionary and Environmental Biology and Inst. of Evolution, Univ. of Haifa, Haifa, Israel. – M. H. M. Menz, Inst. of Ecology and Evolution, Univ. of Bern, Bern, Switzerland and School of Biological Sciences, Univ. of Western Australia, Crawley, Perth, Australia. – A. Aurbach, Laboratory for Energy Conversion, ETH Zurich, Zurich, Switzerland. – S. A. Cabrera-Cruz and J. J. Buler, Dept of Entomology and Wildlife Ecology, Univ. of Delaware, Newark, DE, USA. – C. E. Wainwright, Corix Plains Inst., Univ. of Oklahoma, Norman, OK, USA. – M. Scacco, Dept of Migration and Immuno-ecology, Max Planck Inst. for Ornithology, Radolfzell, Germany. – M. Ciach, Dept of Forest Biodiversity, Univ. of Agriculture, Kraków, Poland. – L. B. Pettersson, Biodiversity Unit, Dept of Biology, Lund Univ., Sweden. – I. Maggini, Konrad-Lorenz Inst. of Ethology, Univ. of Veterinary Medicine Vienna, Wien, Austria. – G. M. Arroyo, Dept of Biology, Univ. of Cadiz, Cadiz, Spain. – D. R. Reynolds, Agriculture, Health and Environment Dept, Natural Resources Inst., Univ. of Greenwich, Chatham, Kent, UK and Computational and Analytical Sciences Dept, Rothamsted Research, Harpenden, UK.

Ecography

42: 942–955, 2019

doi: 10.1111/ecog.03995

Subject Editor: Silke Bauer

Editor-in-Chief: Miguel Araújo

Accepted 22 January 2019



www.ecography.org

Migratory animals are affected by various factors during their journeys, and the study of animal movement by radars has been instrumental in revealing key influences of the environment on flying migrants. Radars enable the simultaneous tracking of many individuals of almost all sizes within the radar range during day and night, and under low visibility conditions. We review how atmospheric conditions, geographic features and human development affect the behavior of migrating insects and birds as recorded by radars. We focus on flight initiation and termination, as well as in-flight behavior that includes changes in animal flight direction, speed and altitude. We have identified several similarities and differences in the behavioral responses of aerial migrants including an overlooked similarity in the use of thermal updrafts by very small (e.g. aphids) and very large (e.g. vultures) migrants. We propose that many aerial migrants modulate their migratory flights in relation to the interaction between atmospheric conditions and geographic features. For example, aerial migrants that encounter cross-wind may terminate their flight or continue their migration and may also drift or compensate for lateral displacement depending on their position (over land, near the coast or over sea). We propose several promising directions for future research, including the development and application of algorithms for tracking insects, bats and large aggregations of animals using weather radars. Additionally, an important contribution will be the spatial expansion of aeroecological radar studies to Africa, most of Asia and South America where no such studies have been undertaken. Quantifying the role of migrants in ecosystems and specifically estimating the number of departing birds from stopover sites using low-elevation radar scans is important for quantifying migrant–habitat relationships. This information, together with estimates of population demographics and migrant abundance, can help resolve the long-term dynamics of migrant populations facing large-scale environmental changes.

Keywords: behavioral responses, bird migration, geographic features, human development, insect migration, meteorological conditions, radar aeroecology

© 2019 The Authors. This is an Online Open article

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Migratory animals are affected by various environmental factors before, during and after their journeys. Specifically, flying migrants have evolved different mechanisms to accomplish their travels by sensing and responding (Bauer et al. 2011, Reynolds et al. 2016) to their dynamic aerial habitat (Womack et al. 2010, Diehl 2013, Reynolds et al. 2018). Inappropriate responses to environmental heterogeneity and dynamics could strongly jeopardize migrant fitness due to direct mortality or through carry-over effects that may lower reproductive output (Newton 2008). Although some important progress has been made in recent years (Krauel et al. 2015, Shamoun-Baranes et al. 2017, Reynolds et al. 2018), we still lack good understanding of how aerial migrants sense and respond to their dynamic habitat.

The study of aerial migratory movements using radar has been instrumental in revealing how environmental factors affect migrants (Kerlinger and Gauthreaux 1985, Riley et al. 1999, Kelly et al. 2012, Bauer et al. 2017). This is because radars may simultaneously track the movement of all animals (that could be as small as aphids of ~0.5 mg) in their range and may operate for decades (Hu et al. 2016, Stepanian and Wainwright 2018). Nevertheless, radars alone cannot usually identify individual species and track migrants for their entire route. Other tracking methods, such as miniaturized GPSs and light-level geolocators, can track a limited number of individual birds and bats for their entire journeys, but cannot track most flying insects (Kissling et al. 2014, but see Wikelski et al. 2006). Due to their size, GPS devices can usually be applied only to relatively large-bodied species, excluding many bird and bat species that are too small to bear the device's weight (Bridge et al. 2011). Geolocators (Bridge et al. 2011) are characterized by a low spatial resolution (dozens to hundreds of kilometers) and a low measurement frequency (one position point per day, at most) (McKinnon et al. 2013). Therefore, radars are an important tool for exploring how environmental conditions affect the behavioral ecology of aerial migrants of almost all sizes at a high rate and spatial resolution (Drake and Reynolds 2012, Chilson et al. 2018, Drake and Bruderer 2018; see also a list of radar types that are being used to track the movement of aerial migrants in Hüppop et al. 2019).

To this end, the present review aims: 1) to synthesize how radar research has contributed to our understanding of behavioral responses of migrants to environmental factors, thereby promoting our knowledge of the causes, mechanisms, patterns and consequences of migratory movements, 2) to identify gaps in our understanding of animal aerocology that could be addressed using radar technology and 3) to offer promising future research directions for using radar to study the aerocology of animal migration. We specifically explore how atmospheric conditions, geographic factors and human development facilitate the initiation and termination of migratory flights, as well as affecting flight speed, direction and altitude choice of migrating insects and birds

Box 1. Extent of radar research on different aerial animal taxa

Searching for keywords in the Scopus® (www.scopus.com) database, we found that bats are an under-studied taxonomic group in radar research, totaling only 78 records, with corresponding figures for insects and birds being 326 and 565 records, respectively. We searched for the following terms in article titles, abstracts and keywords: 'insect' AND 'radar'; 'bird' AND 'radar'; and 'bat' AND 'radar'. Adding the term 'migration' (e.g. 'insect' AND 'radar' AND 'migration') resulted in 31, 122 and 1 records of migration studies using radar of insects, birds and bats, respectively. The search period was from 1956 until 2018 (accessed: 20th March 2018). Since only a single published article deals with bat migration as detected by radar (Stepanian and Wainwright 2018), we could not include bats in the present review despite their important services and functions in various ecosystems, including seed dispersal, pollination and pest control (Medellin and Gaona 1999, Shilton et al. 1999, Aziz et al. 2017, Medellin et al. 2017). We hope that future advances in radar technology and data analysis will spur on future research on bat migration.

(but not bats, Box 1). In addition, we discuss similarities and differences in behavioral responses to environmental conditions between different taxa of migrating animals. We further highlight the importance of interactions between geographic features and atmospheric conditions that modulate the behavior of aerial migrants and suggest that improved radar technology, data analysis and increased geographic coverage of radar studies may advance our understanding of animal–habitat relationships and the role of migrants in ecosystems. Furthermore, we emphasize the need for future research to be directed towards long-term and large-scale studies that can reveal the combined effects of large-scale environmental changes on migrant populations.

Behavioral responses to environmental conditions

The migration journey includes specific sequential stages: initiation or departure, cross-country flight or 'transmigration' and termination. This sequence is repeated if migration is suspended at intermittent stopover sites. Each of these stages presumably requires the sensing of specific cues under a variety of environmental conditions and necessitates the application of specific decision rules to be accomplished (Bauer et al. 2011). The decision by animals to initiate flight, to terminate it and to behave in a certain way during in-flight migratory phases by changing their speed, direction and altitude depends on several endogenous and exogenous factors. These factors include the animal's state, the properties of the resting site and the ambient meteorological conditions. The animal's behavioral decisions have consequences for fitness through their effects on survival, metabolism, navigation and the timing of migration (Alerstam 1991, Liechti

2006, Chapman et al. 2010, Mouritsen 2018), as well as on reproduction, which often follows migration periods within the animal's annual routine (McNamara et al. 1998). In this section, we discuss the migrants' behavioral responses as recorded by radars. These responses are broadly divided into two categories: 1) flight initiation, termination and migration intensity; and 2) in-flight behavior, which includes changes in speed, direction and altitude. We review these responses for insects and birds, highlighting similarities and differences in the responses of these two taxa while noting the extent of available empirical information about these responses. Behavioral responses of migrants acquired by radar are discussed in relation to atmospheric conditions, grouped into three meteorological categories: 1) wind, 2) precipitation, clouds and fog and 3) temperature and thermal updrafts. Additionally, the responses of aerial migrants are discussed with regards to three geographic features: 1) topography, 2) water–land interface and 3) human and infrastructure development (Table 1, 2). Furthermore, we provide an online Supplementary material Appendix 1 with detailed information on behavioral responses of insects and birds, in relation to the aforementioned environmental attributes.

Flight initiation, termination and migration intensity

When to begin or end a migratory flight is an important decision for animal fitness. This decision may consider prevailing

and expected external factors such as ambient temperature and wind direction, internal factors such as the animal's fuel stores and innate motivation, as well as the geographical context, for example the position of the animal in relation to wide ecological barriers such as seas and deserts. We discuss below how flight initiation, termination and migration intensity varies in response to different atmospheric and geographic factors (Table 1, Supplementary material Appendix 1).

Atmospheric conditions

Atmospheric conditions may constrain but could also assist migrating insects and birds. Using information regarding current and expected atmospheric conditions when deciding to depart or land may increase survival and the chance to land in a suitable area while decreasing the animal's metabolic cost of transport. Wind speed and direction have pronounced effects on migratory departure and landing in insects and birds, and consequently these may affect the intensity of migration aloft (Rose et al. 1985, Dokter et al. 2011, Chapman et al. 2015a, chapter 11 in Drake and Reynolds 2012, Hu et al. 2016, Nilsson et al. 2019).

Precipitation inhibits take-off in both insects and birds, and induces flight termination in many cases (chapter 11 in Drake and Reynolds 2012, but see Drake et al. 1981). Precipitation is a term that ranges from drizzle to cloudburst events, including hail and snow. How flying migrants react to these different types of precipitation is not well documented.

Table 1. Flight initiation and termination and migration intensity of migrating insects and birds in response to different meteorological conditions and geographic features.

Behavior	Flight initiation/termination and migration intensity	
	Insects	Birds
Wind (micro-meso-scale)	Tailwinds induce departure and high migration intensity Likely, flight termination and risk of fatalities with extreme winds (hurricanes, tornados)	
Wind associated with other atmospheric conditions (synoptic scale)	Autumn departure associated with the passage of cold fronts and high-altitude winds	Spring: Departure near the centers of high pressure areas and in southerlies – or northerlies for the austral hemisphere (tailwinds). Autumn: Departure close to high pressure areas shortly after the passage of cold fronts
Precipitation, clouds and fog	Heavy rain may inhibit departure and induce termination of flight, but consider related effects with rainy weather: decreasing temperature, weaker or absent thermal convection and strong downdrafts. Insects: Fog was found often in association with relatively calm conditions at the surface and intensive migration aloft, but its effects are not well understood	
Temperature and thermal updrafts	Take-off when temperatures are above 10°C, but some large insects (e.g. moths) can fly at lower temperatures (~5°C). Falling temperatures in autumn promote migratory flight initiation	Variation in temperature promotes take-off, highest intensities in days with warmest temperature in spring
Topography	No studies	No studies about effects on initiation/termination. Migration intensity is lower over complex terrain than in lowlands.
Water–land interface	Cues which normally cause flight termination are overridden when flying over water	Stop over before and after crossing a water body
Human and infrastructure development	Artificial lights attract insects and may stop migratory flights	Artificial lights attract birds and may stop migratory flights, as well as collisions with wind farms. Nocturnal migrants: Stop over in city parks and collision with wind farms

Table 2. Changes in flight airspeed, direction and altitude of migrating insects and birds in response to different meteorological conditions and geographic features.

Behavior	In-flight behavior (speed, direction, altitude)	
	Insects	Birds
Environmental condition/taxa		
Wind (micro-meso-scale)	Animal airspeed increases in headwinds. Lateral drift by crosswinds, but also partial or complete compensation Altitudinal layering by favorable wind Migrants try to avoid storms, but hurricanes and typhoons can trap and transport them (see Box 3 for a classification of flying animals in relation to airflow)	
Wind associated with other atmospheric conditions (synoptic scale)	Synoptic weather associated with the winds (particularly air temperature, and the likelihood of precipitation) will facilitate or impede insect migration	Magnitude and direction of large scale horizontal temperature gradients affects the relative gain in wind assistance that nocturnal migrants can obtain through ascending
Precipitation, clouds and fog	Light rain does not affect flight of large insects; insects can avoid heavier rain by gaining altitude (not intentionally), and found themselves flying outside the cumulonimbus cells	Fog and low clouds can disturb visibility and affect orientation. Effects of precipitation on flight performance are unclear, likely negative
Temperature and thermal updrafts	Insects and birds may disregard temperature variation. Use of strong thermals to soar or ascend and glide or actively fly downward (insects : locusts, butterflies and dragonflies; birds : soaring–gliding birds; Box 3). Soaring–gliding birds : Increase flight speed and altitude in the hottest hours of the day. Nocturnal birds : Selection of travelling altitude according to a compromise between not too cold temperature and slight wind support	
Topography	No radar studies (but see Lack and Lack 1951, and chapter 11 in Drake and Reynolds 2012)	Funneling effect through mountain valleys. Flapping birds : Headwinds favor circumvention of complex terrain, tailwinds favor crossing over it. Soaring migrants : Exploit orographic uplifts
Water–land interface	Large insects : Partial compensation for drifting over the sea. Small insects : Subject to drift. Adaptive drift can increase migration distance by 40%. Large-scale migration over the sea is known	When flying on land along coastlines compensation for lateral drift towards the sea. Flapping birds : Usually cross water bodies, better with tailwinds but also with opposite winds. Soaring migrants : Usually no crossing (or cross with tailwinds), and circumvent water bodies. Seabirds : Reduce the effects of headwinds by flying closer to the coast, and further away with tailwinds
Human and infrastructure development	Insects in steady nocturnal migration at high altitudes are not affected by lights on the ground, with some exceptions	Nocturnal migrants : Re-orientation towards the most intense city skyglow, with risky consequences of collision. Diurnal migrants : Avoidance of wind farms, but high risk of collision

Large insects and birds can keep flying under light rain and drizzle, but heavy rain physically hampers the flight for insects by inflicting high forces of the rain drops on their bodies and wings. Heavy, widespread rainfall also inhibits bird flight initiation and induces its termination (Richardson 1978a, 1990). Yet, one must bear in mind that radars are limited in their ability to detect biological targets under rainfall and thus their usefulness for studying animal behavior under rainy conditions is low (Box 2). The effects of fog on flight initiation and termination are not well understood, and despite its potential significance on migration timing, hardly any empirical data exist (but see Feng et al. 2006).

Temperature variations can be critical for take-off and maintenance of flight in insects. Because insects are poikilotherms, temperature requirements for flight must be

satisfied before flight can be commenced (chapter 9 in Drake and Reynolds 2012) and insects usually have a threshold temperature below which flight cannot be initiated and/or maintained (Dudley 2000, chapter 9 in Drake and Reynolds 2012). In nocturnally migrating birds, flight ability is not limited by temperature, but increasing temperatures in spring and decreasing temperatures in autumn promote departure from staging sites and increase migration intensity (Richardson 1978a, 1990, Van Doren and Horton 2018). Soaring birds depend on thermal updrafts forming in the boundary layer during the day (Spaar and Bruderer 1996, 1997), and thermal convection is probably important for some butterflies that are adapted to soaring flight (Gibo and Pallett 1979). Yet, there are currently no empirical data from radar studies regarding the effect of thermal updrafts

Box 2. Methodological challenges and limitations of radar technology to study environmental effects on animal migration

The effects of various meteorological conditions on migrating insects and birds is now much better understood than in the past, yet some important aspects are still unknown partly due to major methodological challenges. We outline several atmospheric conditions, geographic features and general limitations that currently limit our ability to better understand the aeroecology of migrating animals.

Atmospheric conditions:

1. Rain – The strong attenuation and masking effects of raindrops at typical radar frequencies makes it difficult to detect biological targets in anything other than the lightest precipitation.
2. Fog – The lack of data on the spatial and temporal properties of fog in meteorological databases limits broad-scale analysis of the effects of fog on migrating animals, and only a handful of small scale studies have been so far done to study these effects (Panuccio et al. 2019).

Geographic features:

1. Topography – Insect echoes on scanning radars at low altitudes are swamped by much stronger ‘clutter’ echoes from ground features in mountainous areas. However, entomological vertical-looking or tracking radars are generally less affected by ground clutter and may thus be applied in the future to address questions related to the effects of topography on migratory departure and termination. In addition, only very few radar studies have so far tracked migrating birds in mountainous areas, and such investigation is important for better understanding how the highly dynamic wind field in these areas affects migrants (Panuccio et al. 2016, Aurbach et al. 2018).

General limitations:

1. Detection of migration at low altitudes – Current dedicated entomological radars can only observe targets from ~150 m above ground level. This results in misrepresentation of a major part of migrating insects that fly at lower altitudes. To overcome this problem, insect radars need to implement a FM-CW, millimeter-wave radar system, which would detect insects flying closer to the ground. A different problem that hinders low elevation detection of flying migrants is the positioning of many radars on high mountains (e.g. Meron radar in Northern Israel; Liechti et al. 2019). It has become clear that much of the migration (e.g. 90% of migration traffic rates) goes undetected in these localities because migration mostly takes place close to the ground.
2. Taxonomic identification – A longstanding issue with radar detection is the lack of precision in identifying and categorizing flying animals. Newly developed radar systems implemented specific algorithms that may classify targets into several broad categories (e.g. insect, passerine, wader, bird flock). A finer identification at the level of a specific taxonomic group (e.g. swifts) or even at the species level will substantially advance our inferences regarding migrant aeroecology (see for example Horvitz et al. 2014 for a radar study in which birds were identified to the species level using an optical device).

on flight initiation and termination of soaring birds and insects.

Geographical features

Empirical studies regarding the effects of geographic features, including topography, the water–land interface and man-made structures, on the initiation, termination and intensity of migration, are rare. Direct effects of topography are not well documented, largely because of the limitations of scanning radar technology in recording meaningful data in mountainous areas (Box 2). However, the use of other types of radars and the combination of radars and other measuring devices might allow better exploring such effects in the future. For example, the funneling of passerine migration through mountain passes and other topographic corridors has been recorded in the Appalachians (Williams et al. 2001) and the Alps (Bruderer and Jenni 1990). To the best of our knowledge, no similar radar data from insects is available. In addition to mountain ranges, wide waterbodies that are located within migration flyways may also affect the intensity of migration. Although nocturnal insect migration is usually

halted by the onset of dawn (Drake and Reynolds 2012), this termination of movement is overridden if insect migrants find themselves over water. Accordingly, the range of insect movement under these circumstances may be considerably extended (Drake et al. 1981, Feng et al. 2009), with associated elevated risks of exhaustion and drowning. Similarly, birds may decide whether to stop, follow the coast or cross the sea by considering the possible fatal consequences of drifting over the sea (Alerstam and Pettersson 1977, Horton et al. 2016a).

In recent centuries, anthropogenic landscape modification has influenced much of the earth’s surface, and light pollution is a clear example (Cabrera-Cruz et al. 2018). Insects and birds are mostly attracted to artificial light and some incidental radar observations have recorded concentrations of insects around lights of large towns (e.g. Wad Madani in Sudan, p. 275 in Drake and Reynolds 2012). Similarly, birds stop over at a disproportionately high rate in large city parks (Buler and Dawson 2014) and nearby highly light-polluted areas (Van Doren et al. 2017, McLaren et al. 2018).

In-flight behavior: speed, direction and altitude

In-flight behavioral responses to different environmental conditions can have direct (e.g. reducing the chance of mortality during flight) or indirect (e.g. improving the physiological state of the individual before reproducing) fitness consequences. These behavioral responses can include changing speed, direction and altitude during flight (Table 2). Insects and birds are subject to physical constraints when it comes to changing their airspeed, and the animal may be able to fully compensate for drift only when its airspeed is higher than that of the surrounding airflow (Box 3). In addition to changes in flight speed and direction, flight altitude selection may facilitate migration by selecting specific atmospheric layers with airflows that align with seasonally preferred migration directions.

Atmospheric conditions

Wind is one of the most important atmospheric factors that affect the flight behavior of insects and birds (Shamoun-Baranes et al. 2017, Reynolds et al. 2018). The optimal response of a flapping migrant to tailwinds is airspeed reduction, to decrease the metabolic cost of flight, while increased airspeed is expected in headwind conditions (Pennycuik 1978). The response of insects to wind conditions is strongly constrained by their low airspeeds (Schaefer 1976, Larkin 1991), which are virtually negligible in small insects. Beside this, overall responses to wind by insects and birds are comparable (Table 2). Migrating insects experiencing crosswinds show a variety of responses, including complete and partial drift (Chapman et al. 2010, 2015a, b, Reynolds et al. 2016). However, the variation of responses depends on the size and flight power of the species and the speed of the airflow (Hu et al. 2016). A variety of responses to crosswinds have also been observed in birds. Such responses depend on bird morphology and the preferred flight mode, as well as the geographic context, for example depending on the proximity

to the coast (Green 2001, Horton et al. 2016b, Becciu et al. 2018). Selection of specific flight altitudes is related to strong wind support both in insects and birds (insects: Drake 1985, Wood et al. 2006, Drake and Reynolds 2012; birds: Bruderer and Liechti 1995, Green 2004, Dokter et al. 2011, Kemp et al. 2013).

Despite the limitations of radar technology to track flying birds and insects in rain (Box 2), some data exist regarding flight behavior in precipitating conditions. Under convective rain, insect flight can continue outside the precipitating cumulonimbus cells (Browning et al. 2011, Leskinen et al. 2011, Drake and Reynolds 2012). Moreover, large insects can continue flying in light rain (Drake et al. 1981). The mechanisms by which precipitation affects the flight of insects and birds are not well understood, and most of our knowledge regarding these mechanisms is based on laboratory studies (Webb and King 1984, Ortega-Jimenez and Dudley 2012, Dickerson et al. 2014). The effects of fog and low clouds on in-flight behavior of migrating animals are poorly studied. We note that due to associated reduced visibility, flight within fog may directly affect orientation and could indirectly alter animal speed and altitude.

Insects and birds can tolerate a broad range of temperatures once they are in flight, but temperature itself does not affect flight speed and direction. Several groups of diurnally-migrating insects and birds exploit convective thermals that are columns of ascending air which lift insects and birds to higher altitude above ground (Box 3, but see Geerts and Miao 2005). These include mainly, but not exclusively, small insects (e.g. aphids) and large birds (e.g. vultures).

Geographical features

The effects of topography on insect flight behavior are understudied in radar research (but see chapter 11 in Drake and Reynolds 2012), probably because entomological radars may not be suitable for recording insect echoes in mountainous environments (Box 2). In ornithology, the use of tracking

Box 3. Categorizing the response of flying animals to airflow

The response of flying animals to different airflow conditions based mostly on radar studies permits the broad categorization of flying migrants into the following four categories:

1. Small insects (e.g. aphids) which can only influence movement by selecting whether to ascend into (and stay in) the atmosphere or not (Wainwright et al. 2017).
2. Large insects that can influence their track to a certain extent (Chapman et al. 2010), but usually orientate and displace roughly downwind (Chapman et al. 2016, Reynolds et al. 2016).
3. Birds and bats which may fly fast enough to overcome adverse winds, but due to the high metabolic cost of this behavior usually avoid such flights (Bruderer and Popa-Lisseanu 2005, Liechti 2006, Horton et al. 2016b, 2018, Shamoun-Baranes et al. 2017).
4. Soaring butterflies, birds and bats that use updrafts to gain altitude and then glide towards their destination (Spaar and Bruderer 1996, 1997, Lindhe-Norberg et al. 2000, Horvitz et al. 2014, Reynolds et al. 2018).

Some of the species included in the last category may switch to flapping flight when atmospheric conditions do not facilitate soaring (Spaar and Bruderer 1997, Meyer et al. 2000, 2003). In the marine environment, the flight modes of seabirds range from dynamic soaring in albatrosses and large petrels to pure flapping flight in auks (Mateos-Rodríguez and Bruderer 2012). Interestingly, the largest (i.e. eagles, vultures, pelicans, storks and albatrosses) and the smallest (i.e. aphids) flying animals mostly ascend on convection while most smaller birds such as passerines and larger insects such as moths, use flapping flight.

radars, and marine scanning radar in some cases has allowed migrants to be recorded in complex terrain. It seems that, in some cases, migrating birds deviate from their regular flight direction to follow local topography through mountain passes (Williams et al. 2001).

Flight over the sea could be risky for many insects and birds, particularly under harsh weather conditions and specifically when strong winds are blowing from land towards the sea. Insects have a predisposition to resist being carried over the sea (Russell and Wilson 1996, Shashar et al. 2005; but see Chapman et al. 2010), unless they are habitual transoceanic migrants (Drake et al. 1981, Feng et al. 2006, 2009). The flight behavior of terrestrial birds is variable in response to the water–land interface, depending on body size, flight mode and prevailing winds (Table 2). Seabirds usually migrate across open waters without apparent barriers to their movements. Yet, in some occasions, such as those experienced when crossing a strait, seabirds may benefit from coastal orographic features during flight (Mateos-Rodríguez and Arroyo 2011). Notably, the flight behavior of seabirds near coasts may vary depending on their flight mode and the direction of the wind (Mateos-Rodríguez and Arroyo 2011).

Despite the well-known attraction of many insects towards artificial lights, insects engaged in steady high altitude nocturnal migration do not appear to be affected by lights on the ground (p. 276 in Drake and Reynolds 2012), with some exceptions (Feng et al. 2009). On-the-ground anthropogenic development has well-known consequences on birds engaged in active migration, and radars have been widely used to study the effect of wind turbines and light pollution on the movement of migrating birds (Table 2). Nocturnally-migrating birds adjust flight directions, altitudes and speeds near wind turbine facilities (Mabee et al. 2006, Cabrera-Cruz et al. 2017). Artificial lights also disrupt the flight of migrating birds (Bruderer et al. 1999, Van Doren et al. 2017, Cabrera-Cruz et al. 2018), particularly under poor weather and low visibility conditions (Larkin and Frase 1988), and could have implications for migrant conservation (Hüppop et al. 2019).

Integration and synthesis

Similarities and differences in behavioral responses to environmental conditions

Migrating insects and birds present similarities and differences when responding to environmental factors (Table 1, 2). Wind is likely to be the most important factor affecting the migration of both insects and birds (Box 3), although the evidence is not unequivocal (Van Doren and Horton 2018). Despite large variations in body size and wing morphology within and between insects and birds, there are shared preferable atmospheric conditions. Winds that blow in the intended direction of migration (i.e. tailwinds) trigger take-off for migratory flights and probably cause peaks of migration intensity aloft (Hu et al. 2016). The capacity of an

individual to reach high airspeed while flying dictates its ability to overcome unwanted movement of the airflow, such that the accomplishment of migration for small insects like aphids is much more dependent on airflow blowing towards the intended goal than for larger insects or birds (Chapman et al. 2011). Among birds, wing morphology, body mass and flight mode are important factors that affect flight flexibility in changing wind conditions (Newton 2008), and the behavioral response to wind permits broad categorization of aerial migrants (Box 3).

In birds, the effects of rain may be indirect via wetting the plumage, leading to increased weight and by impeding visibility (Emlen and Demong 1978, Liechti 1986). Insects, and probably birds as well, avoid heavy rain events by tumbling downward before reaching the powerful updrafts associated with thunderstorms that can cause mortality due to freezing (Browning et al. 2011). Precipitation is known to induce flight termination in migrating insects (chapter 11 in Drake and Reynolds 2012, Reynolds et al. 2018), but evidence from birds is rare.

The effects of fog and low clouds on aerial migrants have rarely been studied. Fog is usually found in calm weather conditions (e.g. weak or no winds) at the ground level and its development might be associated with good conditions for insect migration (Feng et al. 2006). Although birds may benefit from the calm weather that is associated with the formation of fog, the low visibility associated with fog may cause disorientation and avoidance of travelling within the fog (Pastorino et al. 2017, Panuccio et al. 2019). We note that precipitation, clouds and fog usually coincide with specific conditions of other atmospheric parameters (e.g. temperature, humidity and wind speed) such that it is often difficult to disentangle their single effects on migrating insects and birds (see below).

The influence of temperature on insect and bird migration has been investigated much more extensively. Insects need warm temperatures to take-off although when flying they can tolerate somewhat lower temperatures, whereas birds are generally more tolerant to both low and high temperatures. A general pattern observed in both insects and birds is that migration is triggered by rising temperature in spring and dropping temperature in autumn (Richardson 1978a, 1990, Mikkola 2003). A consequence of solar radiation is the formation of thermal convection in the diurnal boundary layer, which is exploited by diurnally-migrating insects and birds. Soaring landbirds are the most evident example of adaptation to such atmospheric phenomenon (Spaar and Bruderer 1996), but also smaller migrants such as aphids and several butterfly species use thermal updrafts to gain altitude during their migratory flights (Schaefer 1976, Wainwright et al. 2017, Box 3).

We note that behavioral responses to weather conditions can be complex. Migratory decisions are often based on multilevel input from the atmosphere. For instance, limited visibility, changes in temperature, wind speed and direction, and the limited availability of convective thermals are all

associated with rainy weather. One or more of these factors may cause migrants to descend or land. In insects, ambient temperatures falling below the flight threshold, cessation of convection (which many diurnal insect migrants require to remain aloft) and strong downdraughts associated with convective rainstorms can force insects to descend or land (Russell 1999, Reynolds et al. 2018). Nocturnal birds on migration reach higher altitude taking advantage of vertical wind shear, which arises in particular synoptic situations related to the magnitude and direction of large-scale horizontal temperature gradients (Dokter et al. 2013). The crossing of large water bodies may challenge flying migrants, invoking various behavioral responses. When flying insects and birds migrate over a large water body, they may react quite differently to cues that normally cause flight termination. Insects usually disregard these cues and continue flying while birds reorient to the closest coast to stop over. This takes place mostly around dawn for nocturnal migrants, and dusk for diurnal migrants (Richardson 1978b, Drake et al. 1981, Feng et al. 2009, Archibald et al. 2017).

The interaction between atmospheric conditions and geographic features in the response of flying migrants

Several behavioral responses to atmospheric conditions are modulated by geographic features, in aerial migrants constituting interactions. A notable example are crosswinds (Fig. 1). Migrating land-birds may drift laterally under crosswind conditions when flying over land far from the coast. Yet, under similar wind conditions, the birds will try overcoming lateral drift when they are found close to the shoreline, presumably to reduce the chances of being carried over the sea, which could be fatal (Horton et al. 2016b, Becciu et al. 2018). Interestingly, nocturnally-migrating insects that usually terminate their flight at dawn continue flying at that time when found over water (Drake et al. 1981, Feng et al. 2006, 2009). Yet, evidence for the modulation of insect flight behavior in relation to wind over land and when flying close or over the sea has not been documented to date. In any case, the low airspeed of insects may result in a low capacity to resist the wind (Drake and Reynolds 2012). Diurnally-migrating dragonflies have also been documented flying in the dark under foggy conditions, which are common during migration events. The insects, which usually halt their migration at or near sunset, probably continued flying because the fog prevented them from seeing the ground and specifically the coastline (Feng et al. 2006).

A different interaction between atmospheric conditions and geographic features relates to bird flight behavior in relation to wind in mountainous areas. Wind was found to modulate the tendency of low-flying birds to circumvent mountains instead of crossing them (Williams et al. 2001), which is more prevalent under headwind conditions when most birds fly at relatively low altitudes (Liechti 1986). Under tailwind conditions, birds usually cross mountain ranges in higher numbers and disregard local topography (Lack and Lack 1951). We note that high resolution wind flow description

and simulation of movement over complex terrain could provide a deeper understanding of the environmental factors faced by travelling birds. In a recent simulation study based on radar data, topography was found to guide the wind flow and consequently changed the profitability of different flight paths due to its effect on flight energy costs (Aurbach et al. 2018). This combined effect of wind and topography therefore leads to concentrations of bird migration at specific flyways under certain meteorological conditions (Aurbach et al. 2018). Although the seasonal near-ground passage of hordes of insects through high mountain passes is well known (Lack and Lack 1951, Aubert et al. 1976; Box 2), no radar studies have documented this phenomenon, but some studies of insect concentration in response to lee waves, topographic wind eddies and rotors (chapter 11 in Drake and Reynolds 2012).

The response of aerial migrants to interactions between atmospheric conditions and man-made structures are largely understudied by radars. Such studies are important for understanding the mechanisms by which anthropogenic structures cause mortality of aerial migrants (Hüppop et al. 2019), for example the attraction of nocturnally-migrating birds to lights on tall towers when flying within low clouds (Larkin and Frase 1988; Fig. 1). Given the abundance of tall anthropogenic structures in many regions in the world, it is important to characterize this interaction and determine measures to mitigate the consequences (Hüppop et al. 2019).

Future directions

Despite the advancement of our understanding of the behavioral responses of migrants in relation to meteorology and geographic features as revealed by radars, there are still substantial gaps in our knowledge that warrant future investigation. In particular, the effects of several environmental factors such as precipitation and fog, landscape topography and man-made structures, are currently understudied. Beyond the need to address the effects of specific environmental factors, we discuss several promising research directions that may be investigated using radars, and which could broadly contribute to our understanding of the aerocology of aerial migrants.

Identifying and tracking of additional taxa by radars

Recently, weather radar networks in Europe and the USA have been successfully applied to study the broad front migration of birds, of which most are songbirds (Dokter et al. 2018, Van Doren and Horton 2018, Nilsson et al. 2019). The application of algorithms to study the movement of birds that congregate in flocks during migration, including waterbirds (e.g. geese and herons) and soaring migrants (e.g. storks and eagles) using weather radar data are largely missing (but see Buler et al. 2012 for a study of over-wintering waterfowl). One of the most important gaps in knowledge relates to the unfortunate scarcity of bat migration research

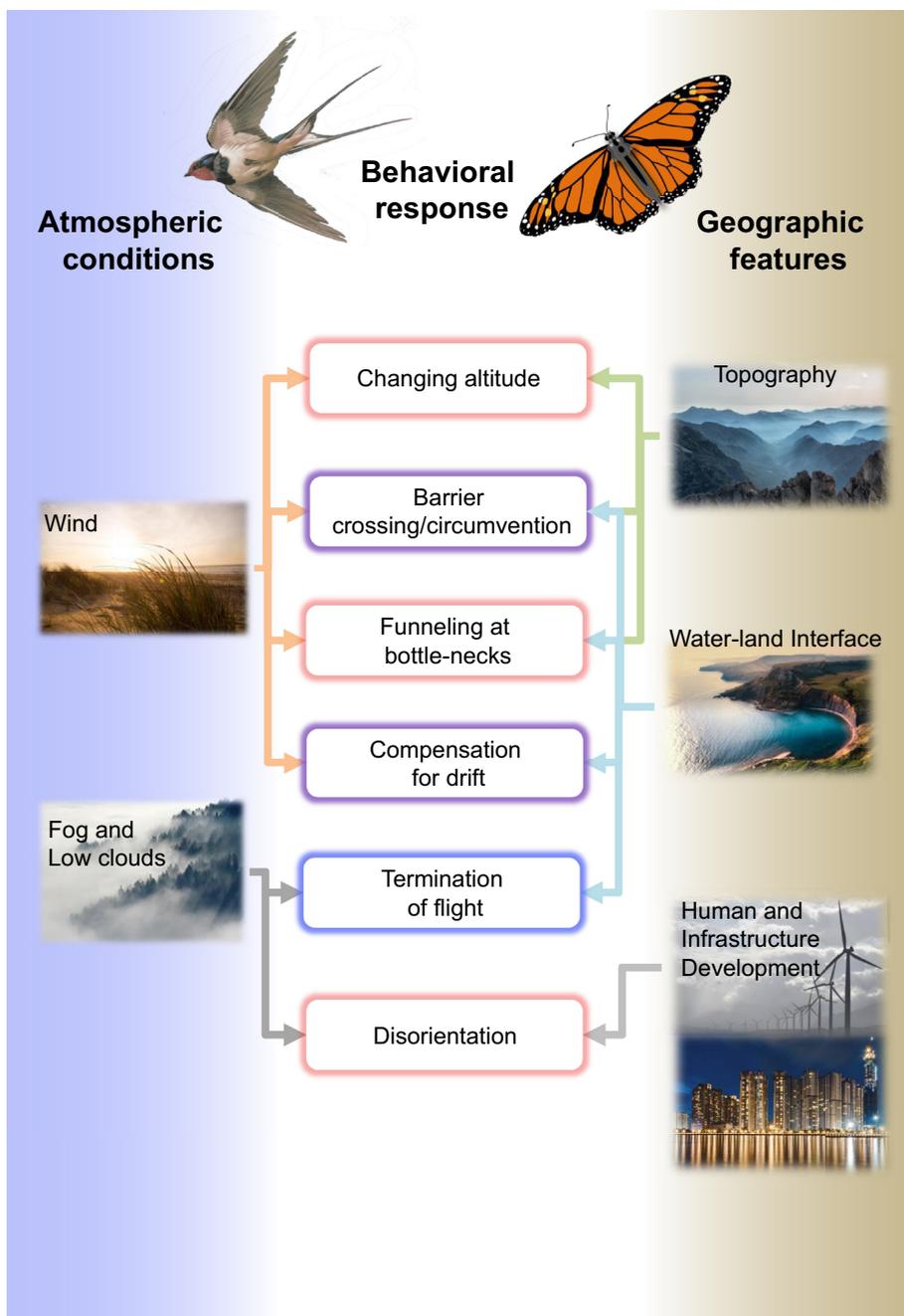


Figure 1. Major behavioral responses of flying migrants caused by the interaction between atmospheric conditions and geographic features as revealed by radar studies. Behavioral responses were found in insects only (blue glow), in birds only (red glow) or in both groups (violet glow). Birds changed their altitude when crossing mountains (Lack and Lack 1951, Williams et al. 2001) and also selected to cross mountains and waterbodies or terminate their flight (in the case of insects; Russell and Wilson 2001, Feng et al. 2009) or circumvent them (in the case of birds; Williams et al. 2001) depending on wind conditions. Similarly, birds funneled in bottle-necks (valleys or peninsulas) that are usually aligned with preferred migration directions of the migrants (Mabee et al. 2006, Aurbach et al. 2018). Flying migrants compensate for wind drift close to coastlines when the wind is blowing towards the sea to avoid the risk to be displaced far offshore (insects: Russell and Wilson 1996, 2001, Chapman et al. 2015a; birds: Richardson 1978b, Horton et al. 2016b). When flying close to the coast or over large waterbodies, fog and low clouds can prevent diurnally-migrating insects from continue flying and terminate their flight above ground, such that their flight extends over water in the night (Feng et al. 2006). Migrating birds that fly in the vicinity of tall illuminated towers and buildings may disorient when low clouds and fog prevail (Larkin and Frase 1988), which may lead to mortality.

(Box 1), particularly given the importance of migratory bats in various ecosystems and their role in insect pest control (McCracken et al. 2012). Another set of algorithms that has already been developed (Chilson et al. 2012, Stepanian et al. 2014, 2016), but have not been largely implemented in data analysis from weather radar networks relates to the detection of insect movements. The future development and implementation of algorithms that will extract data from a wider diversity of aerial taxa may substantially improve our ability to study how these animals are affected by environmental conditions. Specifically, the development and application of algorithms to detect insects in weather radars is expected to revolutionize our capacity to quantify insect migration by allowing a spatially expansive investigation of insect movement across entire continents. Such development will enhance our ability to quantify their flux and roles in various natural and agricultural systems (Hu et al. 2016). Notably, the development and application of the aforementioned algorithms will allow comprehensive cross-taxa comparisons of the responses of aerial migrants to environmental conditions. Moreover, algorithms that will detect and track bird flocks at real time using data from weather radars may improve existing warning systems and will further reduce the collisions of aerial migrants with civil and military aviation (van Gasteren et al. 2019).

Increasing the coverage of aeroecological radar studies

Unlike the study of migrant aeroecology using local radars and large-scale networks of weather radars in the United States (i.e. NEXRAD) and Europe (i.e. OPERA), which successfully monitor mass movements of aerial organisms over regional (Dokter et al. 2011, Farnsworth et al. 2016, Hu et al. 2016) and continental scales (Lowery and Newman 1966, Van Doren and Horton 2018, Nilsson et al. 2019), the scarcity of radar studies from the African continent, most of Asia and South America limits our knowledge of animal aeroecology in these vast areas. The development of processing and analytical methodologies, as well as knowledge sharing and inter-disciplinary data integration for identifying and tracking aerial migrants across Europe was conducted by the COST (European Cooperation in Science and Technology) action ENRAM (European Network for the Radar surveillance of Animal Movement in Europe; <www.enram.eu>) during 2013–2017. Using data from existing radar networks in additional regions of the world where such networks exist (e.g. India and China) is a promising way to increase the geographic coverage of animal migration research and for exploring migrant aeroecology in various systems (Hüppop et al. 2019). Nevertheless, we note that studies involving local radars are extremely useful for researching migration properties that cannot be studied using weather radars, including the identification of the species involved in some cases (Horvitz et al. 2014), the extraction of animal wingbeat frequency (Bruderer and Popa-Lisseanu 2005) and detailed flight trajectories (Larkin and Frase 1988). Local radars are also important for cross-calibrating weather radar systems (Nilsson et al. 2018, Liechti et al. 2019). Moreover, the use

of additional existing meteorological measuring platforms, such as wind profilers, is a promising direction to substantially increase our knowledge of aerial migration in different parts of the world (Weisshaupt et al. 2018). We note that seabirds have been mostly tracked with radars from the coast, but recently a study showing seabird foraging movements and social interactions was done using radar on board a fishing vessel (Assali et al. 2017). The use of shipborne radars for tracking bird migration across seas could allow for the exploration of novel research questions, such as the effects of human-induced food resources on migrating seabirds far from the shore. Airborne radars can be an important tool and have previously been used to detect insect migration and successfully describe their behavioral responses to atmospheric conditions (Geerts and Miao 2005, but see also chapter 11 in Drake and Reynolds 2012). This type of radar can be used to cover areas where it is not possible to use land-based radars (e.g. over sea).

Quantifying the role of migrants in ecosystems

We propose that quantifying the abundance and distribution of migrating animals using radars is a first critical step for better understanding their roles in ecosystem functions and services. This is because migrants interact with organisms in different ecosystems and participate in massive biological transport processes of nutrients and energy (Bauer and Hoyer 2014, Bauer et al. 2017). Knowledge regarding the abundance and distribution of migrants is important for understanding their ecology and could be critical for their conservation (Hüppop et al. 2019). Recently, substantial progress has been made with radar-based calculations of transport phenomena involving both migrating insects (Hu et al. 2016) and birds (Dokter et al. 2018, Horton et al. 2019), but such studies are still very rare.

Despite the importance of characterizing animal–habitat associations, only a few studies have so far estimated the densities of migrating birds departing from stopover sites using weather radars. These studies were done using low-elevation radar scans that allowed quantifying the number of departing birds from areas that are within the coverage range of the radar. To date, all these studies were made in North America (Bonter et al. 2009, Buler and Dawson 2014, Lafleur et al. 2016). Further application of this approach may help in assessing the importance of different land uses, habitat types and geographic features on migrating birds in different parts of the world. Importantly, quantifying large-scale habitat relationships of migrants may aid their conservation by assessing their habitat selection criteria (Buler and Dawson 2014). Moreover, these studies allow reconciling large-scale migration patterns of migrants that are tracked in mid-air with departure decisions of individual animals, thereby exposing the mechanisms by which environmental factors act on the decision of individual animals to depart from stopover sites and continue their migration aloft. In this context, it would be of interest to investigate if mass migration events are the consequence of a synchronized take-off

of a huge number of migrants (for example, under certain atmospheric conditions). Interestingly, radar data, especially those collected over many years, may allow the response of migrants to both habitat degradation and habitat restoration activities to be measured (Sieges et al. 2014). Furthermore, we note that forecasting high intensity insect (Hu et al. 2016) and bird (Van Doren and Horton 2018) migration over large spatial scales is important for characterizing the properties of migrant-related transport processes, including their dynamics, practical implications (e.g. mass migration of agricultural pests), and future fate under different environmental change scenarios.

Investigating the long-term and large-scale effects of environmental changes on migrant populations

Long-term radar data collection facilitates the investigation of migrant aeroecology at multiple scales in time (from hours to seasons, years and decades) and space (from a single site to a region and an entire continent). Using long-term data to infer population properties over a continental scale is particularly important for analyzing population trends in the light of ongoing global environmental changes (Kelly et al. 2012, Stepanian and Wainwright 2018). A recent example of the successful application of this approach involves the quantification of demographic indices for the entire population of migrating birds in North America (Dokter et al. 2018). A different approach that produced interesting results combined estimates of future climates with knowledge regarding the response of migrants to atmospheric variables from radar data. This work was able to predict the future properties (e.g. spatial distribution and temporal characteristics) of land-bird migration over North America under projected climate change scenarios (La Sorte et al. 2018). Due to the overall scarcity of long-term analyses of phenological patterns and population dynamics across wide geographic areas, we suggest directing future research efforts towards the long-term and broad-scale investigation of migration patterns in areas where data from radar networks are readily available. Scientists can now use this research framework to investigate how future changes in major environmental conditions (e.g. warming air temperatures; Van Doren and Horton 2018) may influence migration properties, with potential consequences for reproductive output and hence population dynamics following the migration period.

A different aspect that can be modeled is the consequences of anthropogenic structures on aerial migrants. Data from radar-based spatially and temporally resolved migration metrics (Aurbach et al. 2018) combined with information about the proposed locality and size of structures such as wind farms, can help to model the impacts of future developments at continental and flyway scales. Furthermore, predictive modelling will facilitate the application of risk mitigation measures to, at least partially, overcome potential negative consequences of human development on migrant populations (Hüppop et al. 2019).

Acknowledgements – We thank all ENRAM – related colleagues for discussions that contributed to the development of this article. We would also like to thank Silke Bauer and two anonymous reviewers for their comments, which substantially improved the manuscript. *Funding* – We acknowledge the support provided by the European Cooperation in Science and Technology (COST) through Action no. ES1305, European Network for the Radar Surveillance of Animal Movement (ENRAM), in facilitating this collaboration.

References

- Alerstam, T. 1991. Bird's flight and optimal migration. – *Trends Ecol. Evol.* 6: 210–215.
- Alerstam, T. and Pettersson, S. G. 1977. Why do migrating birds fly along coastlines? – *J. Theor. Biol.* 65: 699–712.
- Archibald, K. M. et al. 2017. Migrating birds reorient toward land at dawn over the Great Lakes, USA. – *Auk* 134: 193–201.
- Assali, C. et al. 2017. Seabird distribution patterns observed with fishing vessel's radar reveal previously undescribed sub-meso-scale clusters. – *Sci. Rep.* 7: 7364.
- Aubert, J. et al. 1976. Douze ans de captures systématiques de Syrphides (Diptères) au col de Bretolet (Alpes valaisannes). – *Mitt. Schweiz. Entomol. Ges.* 49: 115–142.
- Aurbach, A. et al. 2018. Complex behaviour in complex terrain. Modelling bird migration in a high resolution wind field across mountainous terrain to simulate observed patterns. – *J. Theor. Biol.* 454: 126–138.
- Aziz, S. A. et al. 2017. Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibethinus*). – *Ecol. Evol.* 7: 8670–8684.
- Bauer, S. and Hoye, B. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. – *Science* 344: 1242552.
- Bauer, S. et al. 2011. Cues and decision rules in animal migration. – In: Milner-Gulland, E. J. et al. (eds), *Animal migration: a synthesis*. – Oxford Univ. Press, pp. 68–87.
- Bauer, S. et al. 2017. From agricultural benefits to aviation safety: realizing the potential of continent-wide radar networks. – *BioScience* 67: 912–918.
- Becciu, P. et al. 2018. Contrasting aspects of tailwinds and asymmetrical response to crosswinds in soaring migrants. – *Behav. Ecol. Sociobiol.* 72: 28.
- Bonter, D. N. et al. 2009. Characteristics of important stopover locations for migrating birds: remote sensing with radar in the Great Lakes Basin. – *Conserv. Biol.* 23: 440–448.
- Bridge, E. S. et al. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. – *BioScience* 61: 689–698.
- Browning, K. A. et al. 2011. Layers of insects echoes near a thunderstorm and implications for the interpretation of radar data in terms of airflow. – *Q. J. R. Meteorol. Soc.* 137: 723–735.
- Bruderer, B. and Jenni, L. 1990. Migration across the Alps. – In: Gwinner, E. (ed.), *Bird migration: physiology and ecophysiology*. – Springer, pp. 60–77.
- Bruderer, B. and Liechti, F. 1995. Variation in density and height distribution of nocturnal migration in the south of Israel. – *Israel J. Zool.* 41: 477–487.
- Bruderer, B. and Popa-Lisseanu, A. 2005. Radar data on wing-beat frequencies and flight speeds of two bat species. – *Acta Chiropterol.* 7: 73–82.

- Bruderer, B. et al. 1999. Behaviour of migrating birds exposed to X-band radar and a bright light beam. – *J. Exp. Biol.* 202: 1015–1022.
- Buler, J. J. and Dawson, D. K. 2014. Radar analysis of fall bird migration stopover sites in the northeastern U.S. – *Condor* 116: 357–370.
- Buler, J. J. et al. 2012. Mapping wintering waterfowl distributions using weather surveillance radar. – *PLoS One* 7: e41571.
- Cabrera-Cruz, S. A. et al. 2017. Patterns of nocturnal bird migration in southern Mexico. – *Rev. Mex. Biodivers.* 88: 867–879.
- Cabrera-Cruz, S. A. et al. 2018. Light pollution is greatest during the migratory phase of the annual cycle for nocturnally migrating birds around the world. – *Sci. Rep.* 8: 3261.
- Chapman, J. W. et al. 2010. Flight orientation behaviors promote optimal migration trajectories in high-flying insects. – *Science* 327: 682–85.
- Chapman, J. W. et al. 2011. Animal orientation strategies for movement in flows. – *Curr. Biol.* 21: R861–R870.
- Chapman, J. W. et al. 2015a. Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. – *Ecol. Lett.* 18: 287–302.
- Chapman, J. W. et al. 2015b. Detection of flow direction in high-flying insect and songbird migrants. – *Curr. Biol.* 25: R733–R752.
- Chapman, J. W. et al. 2016. Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. – *J. Anim. Ecol.* 85: 115–124.
- Chilson, P. B. et al. 2012. Estimating animal densities in the atmosphere using weather radar: to Z or not to Z? – *Ecosphere* 3: 72.
- Chilson, P. B. et al. 2018. Radar aeroecology. – In: Chilson, P. B. et al. (eds), *Aeroecology*. – Springer, pp. 277–309.
- Dickerson, A. K. et al. 2014. Raindrops push and splash flying insects. – *Phys. Fluids* 26: 027104.
- Diehl, R. H. 2013. The airspace is habitat. – *Trends Ecol. Evol.* 28: 377–379.
- Dokter, A. M. et al. 2011. Bird migration flight altitudes studied by a network of operational weather radars. – *J. R. Soc. Interface* 8: 30–43.
- Dokter, A. M. et al. 2013. High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. – *PLoS One* 8: e52300.
- Dokter, A. M. et al. 2018. Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. – *Nat. Ecol. Evol.* 2: 1603–1609.
- Drake, V. A. 1985. Radar observations of moths migrating in a nocturnal low-level jet. – *Ecol. Entomol.* 10: 259–265.
- Drake, V. A. and Bruderer, B. 2018. Aeroecological observation methods. – In: Chilson, P. B. et al. (eds), *Aeroecology*. – Springer, pp. 201–237.
- Drake, V. A. and Reynolds, D. R. 2012. Radar entomology: observing insect flight and migration. – CABI.
- Drake, V. A. et al. 1981. Insect migration across Bass Strait during spring: a radar study. – *Bull. Entomol. Res.* 90: 545–571.
- Dudley, R. 2000. *The biomechanics of insect flight: form, function, evolution*. – Princeton Univ. Press.
- Emlen, S. T. and Demong, N. J. 1978. Orientation strategies used by free-flying bird migrants: a radar tracking study. – In: Schmidt-Koenig, K. and Keeton, W. T. (eds), *Animal migration, navigation and homing*. – Springer, pp. 283–293.
- Farnsworth, A. et al. 2016. A characterization of autumn nocturnal migration detected by weather surveillance radars in the northeastern USA. – *Ecol. Appl.* 26: 752–770.
- Feng, H. Q. et al. 2006. Nocturnal migration of dragonflies over the Bohai Sea in northern China. – *Ecol. Entomol.* 31: 511–520.
- Feng, H. Q. et al. 2009. Seasonal migration of *Helicoverpa armigera* (Lepidoptera: Noctuidae) over the Bohai Sea. – *J. Econ. Entomol.* 102: 95–104.
- Geerts, B. and Miao, Q. 2005. Airborne radar observations of the flight behavior of small insects in the atmospheric convective boundary layer. – *Environ. Entomol.* 34: 361–377.
- Gibo, D. L. and Pallett, M. J. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. – *Can. J. Zool.* 57: 1393–1401.
- Green, M. 2001. Is wind drift in migrating barnacle and brent geese, *Branta leucopsis* and *Branta benicla*, adaptive or non-adaptive? – *Behav. Ecol. Sociobiol.* 50: 45–54.
- Green, M. 2004. Flying with the wind – spring migration of arctic-breeding waders and geese over South Sweden. – *Ardea* 92: 145–159.
- Horton, K. G. et al. 2016a. Where in the air? Aerial habitat use of nocturnally migrating birds. – *Biol. Lett.* 12: 20160591.
- Horton, K. G. et al. 2016b. Nocturnally migrating songbirds drift when they can and compensate when they must. – *Sci. Rep.* 6: 21249.
- Horton, K. G. et al. 2018. Navigating north: how body mass and winds shape avian flight behaviours across a North American migratory flyway. – *Ecol. Lett.* 21: 1055–1064.
- Horton, K. G. et al. 2019. Holding steady: little change in intensity or timing of bird migration over the Gulf of Mexico. – *Global Change Biol.* doi: 10.1111/gcb.14540.
- Horvitz, N. et al. 2014. The gliding speed of migrating birds: slow and safe or fast and risky? – *Ecol. Lett.* 17: 670–679.
- Hu, G. et al. 2016. Mass seasonal bioflows of high-flying insect migrants. – *Science* 354: 1584–1587.
- Hüppop, O. et al. 2019. Perspectives and challenges for the use of radar in biological conservation. – *Ecography* 42: 912–930.
- Kelly, J. F. et al. 2012. Quantifying animal phenology in the atmosphere at a continental scale using NEXRAD weather radars. – *Ecosphere* 3: 16.
- Kemp, M. U. et al. 2013. The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. – *Ibis* 155: 734–749.
- Kerlinger, P. and Gauthreaux, S. A. 1985. Seasonal timing, geographic distribution and flight behavior of broad-winged hawks during spring migration in South Texas: a radar and visual study. – *Auk* 102: 735–743.
- Kissling, W. D. et al. 2014. Challenges and prospects in the telemetry of insects. – *Biol. Rev.* 89: 511–530.
- Krauel, J. J. et al. 2015. Weather-driven dynamics in a dual-migrant system: moths and bats. – *J. Anim. Ecol.* 84: 604–614.
- Lack, D. and Lack, E. 1951. Migration of insects and birds through a pyrenean pass. – *J. Anim. Ecol.* 20: 63–67.
- Lafleur, J. M. et al. 2016. Geographic position and landscape composition explain regional patterns of migrating landbird distributions during spring stopover along the northern coast of the Gulf of Mexico. – *Landscape Ecol.* 31: 1697–1709.
- Larkin, R. P. 1991. Flight speeds observed with radar, a correction: slow 'birds' are insects. – *Behav. Ecol. Sociobiol.* 29: 221–224.

- Larkin, R. P. and Frase, B. A. 1988. Circular paths of birds flying near a broadcasting tower in cloud. – *J. Comp. Psychol.* 102: 90–93.
- La Sorte, F. A. et al. 2018. Projected changes in wind assistance under climate change for nocturnally migrating bird populations. – *Global Change Biol.* 25: 598–601.
- Leskinen, M. et al. 2011. Pest insect immigration warning by an atmospheric dispersion model, weather radars and traps. – *J. Appl. Entomol.* 135: 55–67.
- Liechti, F. 1986. Einfluss der lokalen topographie auf nachtlich ziehende Vogel. – *Ornithol. Beob.* 83: 35–66.
- Liechti, F. 2006. Birds: blowin' by the wind? – *J. Ornithol.* 147: 202–211.
- Liechti, F. et al. 2019. Cross-calibration of different radar systems for monitoring nocturnal bird migration across Europe and the Near East. – *Ecography* 42: 887–898.
- Lindhe-Norberg, U. M. et al. 2000. Soaring and non-soaring bats of the family Pteropodidae (flying foxes, *Pteropus* spp.): wing morphology and flight performance. – *J. Exp. Biol.* 203: 651–664.
- Lowery, G. H. Jr. and Newman, R. J. 1966. A continent wide view of bird migration on four nights in October. – *Auk* 83: 547–586.
- Mabee, T. et al. 2006. Nocturnal bird migration over an appalachian ridge at a proposed wind power project. – *Wildl. Soc. Bull.* 34: 682–690.
- Mateos-Rodríguez, M. and Arroyo, G. M. 2011. Ocean surface winds drive local-scale movements within long-distance migrations of seabirds. – *Mar. Biol.* 158: 329–339.
- Mateos-Rodríguez, M. and Bruderer, B. 2012. Flight speeds of migrating seabirds in the strait of gibraltar and their relation to wind. – *J. Ornithol.* 153: 881–889.
- McCracken, G. F. et al. 2012. Bats track and exploit changes in insect pest populations. – *PLoS One* 7: e43839.
- McKinnon, E. A. et al. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. – *Auk* 130: 211–222.
- McLaren, J. D. et al. 2018. Artificial light confounds broad-scale habitat use by migrating birds. – *Ecol. Lett.* 21: 356–364.
- McNamara, J. et al. 1998. The timing of migration within the context of an annual routine. – *J. Avian Biol.* 29: 416–423.
- Medellin, R. A. and Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. – *Biotropica* 31: 478–485.
- Medellin, R. A. et al. 2017. Conservation relevance of bat caves for biodiversity and ecosystem services. – *Biol. Conserv.* 211: 45–50.
- Meyer, S. K. et al. 2000. To cross the sea or to follow the coast? Flight directions and behaviour of migrating raptors approaching the Mediterranean Sea in autumn. – *Behaviour* 137: 379–399.
- Meyer, S. K. et al. 2003. Sea crossing behaviour of falcons and harriers at the southern Mediterranean coast of Spain. – *Avian Sci.* 3: 153–162.
- Mikkola, K. 2003. Red admirals *Vanessa atalanta* (Lepidoptera: Nymphalidae) select northern winds on southward migration. – *Entomol. Fenn.* 14: 15–24.
- Mouritsen, H. 2018. Long-distance navigation and magnetoreception in migratory animals. – *Nature* 558: 50–59.
- Newton, I. 2008. The migration ecology of birds. – Academic Press.
- Nilsson, C. et al. 2019. Revealing patterns of nocturnal migration using the European weather radar network. – *Ecography* 42: 876–886.
- Nilsson, C. et al. 2018. Field validation of radar systems for monitoring bird migration. – *J. Appl. Ecol.* 55: 2552–2564.
- Ortega-Jiménez, V. M. and Dudley, R. 2012. Flying in the rain: hovering performance of Anna's Hummingbirds under varied precipitation. – *Proc. R. Soc. B* 279: 3996–4002.
- Panuccio, M. et al. 2016. Radar tracking reveals influence of cross-winds and topography on migratory behavior of European honey buzzards. – *J. Ethol.* 34: 73–77.
- Panuccio, M. et al. 2019. Migrating birds avoid flying through fog and low clouds. – *Int. J. Biometeorol.* doi: 10.1007/s00484-018-01656-z.
- Pastorino, A. et al. 2017. Fog and rain lead migrating White storks *Ciconia ciconia* to perform reverse migration and to land. – *Avocetta* 41: 5–12.
- Pennycook, C. J. 1978. Fifteen testable predictions about bird flight. – *Oikos* 30: 165–176.
- Reynolds, A. M. et al. 2016. Orientation in high-flying migrant insects in relation to flows: mechanisms and strategies. – *Phil. Trans. R. Soc. B* 371: 20150392283.
- Reynolds, D. R. et al. 2018. Riders on the wind: the aeroecology of insect migrants. – In: Chilson, P. B. et al. (eds), *Aeroecology*. – Springer, pp. 145–177.
- Richardson, W. J. 1978a. Timing and amount of bird migration in relation to weather: a review. – *Oikos* 30: 224–272.
- Richardson, W. J. 1978b. Reorientation of nocturnal landbird migrants over the Atlantic ocean near Nova Scotia in Autumn. – *Auk* 95: 717–732.
- Richardson, W. J. 1990. Timing and amount of bird migration in relation to weather: updated review. – In: Gwinner, E. (ed), *Bird migration: physiology and ecophysiology*. – Springer, pp. 78–101.
- Riley, J. R. et al. 1999. Compensation for wind drift by bumblebees. – *Nature* 400: 126.
- Rose, D. J. W. et al. 1985. Downwind migration of the African armyworm moth, *Spodoptera exempta*, studied by mark-and-capture and by radar. – *Ecol. Entomol.* 10: 299–313.
- Russell, R. W. 1999. Precipitation scrubbing of aerial plankton: inferences from bird behaviour. – *Oecologia* 118: 381–387.
- Russell, R. W. and Wilson, J. W. 1996. Aerial plankton detected by radar. – *Nature* 381: 200–201.
- Russell, R. W. and Wilson, J. W. 2001. Spatial dispersion of aerial plankton over east-central Florida: aeolian transport and coastline concentrations. – *Int. J. Remote Sens.* 22: 2071–2082.
- Schaefer, G. W. 1976. Radar observations of insect flight. – In: Rainey, R. C. (ed), *Insect flight, symposia of the royal entomological society of London*, no. 7. – Blackwell, pp. 157–197.
- Shamoun-Baranes, J. et al. 2017. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. – *J. Comp. Physiol. A* 203: 509–529.
- Shashar, N. et al. 2005. Migrating locusts can detect polarized reflections to avoid flying over the sea. – *Biol. Lett.* 1: 472–475.
- Shilton, L. A., et al. 1999. Old world fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. – *Proc. R. Soc. B* 266: 219–223.
- Sieges, M. L. et al. 2014. Assessment of bird response to the migratory bird habitat initiative using weather-surveillance radar. – *Southeast. Nat.* 13: 36–65.
- Spaar, R. and Bruderer, B. 1996. Soaring migration of Steppe Eagles *Aquila nipalensis* in southern Israel: flight behaviour under various wind and thermal conditions. – *J. Avian Biol.* 27: 289–301.

- Spaar, R. and Bruderer, B. 1997. Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. – Behav. Ecol. 8: 288–297.
- Stepanian, P. M. and Wainwright, C. E. 2018. Ongoing changes in migration phenology and winter residency at Bracken Bat Cave. – Global Change Biol. 24: 3266–3275.
- Stepanian, P. M. et al. 2014. An introduction to radar image processing in ecology. – Methods Ecol. Evol. 5: 730–738.
- Stepanian, P. M. et al. 2016. Dual-polarization radar products for biological applications. – Ecosphere 7: e01539.
- Van Doren, B. and Horton, K. G. 2018. A continental system for forecasting bird migration. – Science 361: 1115–1118.
- Van Doren, B. et al. 2017. High-intensity urban light installation dramatically alters nocturnal bird migration. – Proc. Natl Acad. Sci. USA 114: 11175–11180.
- van Gasteren, H. et al. 2019. Aeroecology meets aviation safety: early warning systems in Europe and the Middle East prevent collisions between birds and aircraft. – Ecography 42: 899–911.
- Wainwright, C. E. et al. 2017. The movement of small insects in the convective boundary layer: linking patterns to processes. – Sci. Rep. 7: 5438.
- Webb, D. R. and King, J. R. 1984. Effects of wetting on insulation of bird and mammal coats. – J. Therm. Biol. 9: 189–191.
- Weisshaupt, N. et al. 2018. The role of radar wind profilers in ornithology. – Ibis 160: 516–527.
- Wikelski, M. et al. 2006. Simple rules guide dragonfly migration. – Biol. Lett. 2: 325–329.
- Williams, T. C. et al. 2001. Bird migration through a mountain pass studied with high resolution radar, ceilometers and census. – Auk 118: 389–403.
- Womack, A. M. et al. 2010. Biodiversity and biogeography of the atmosphere. – Phil. Trans. R. Soc. B 365: 3645–3653.
- Wood, C. R. et al. 2006. The influence of the atmospheric boundary layer on nocturnal layers of moths migrating over southern Britain. – Int. J. Biometeorol. 50: 193.

Supplementary material (available online as Appendix ecog-03995 at <www.ecography.org/appendix/ecog-03995>). Appendix 1.