ECOGRAPHY

Review and synthesis

Environmental effects on flying migrants revealed by radar

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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 identi-fied 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, includ-ing 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 demo-graphics 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

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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 aeroecology that could be addressed using radar technology and 3) to offer promising future research directions for using radar to study the aeroecology 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 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	
Environmental condition/taxa	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 downdraughts. **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)	
Environmental condition/taxa	Insects	Birds
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 (Pennycuick 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 under-studied 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

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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 aeroecology 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
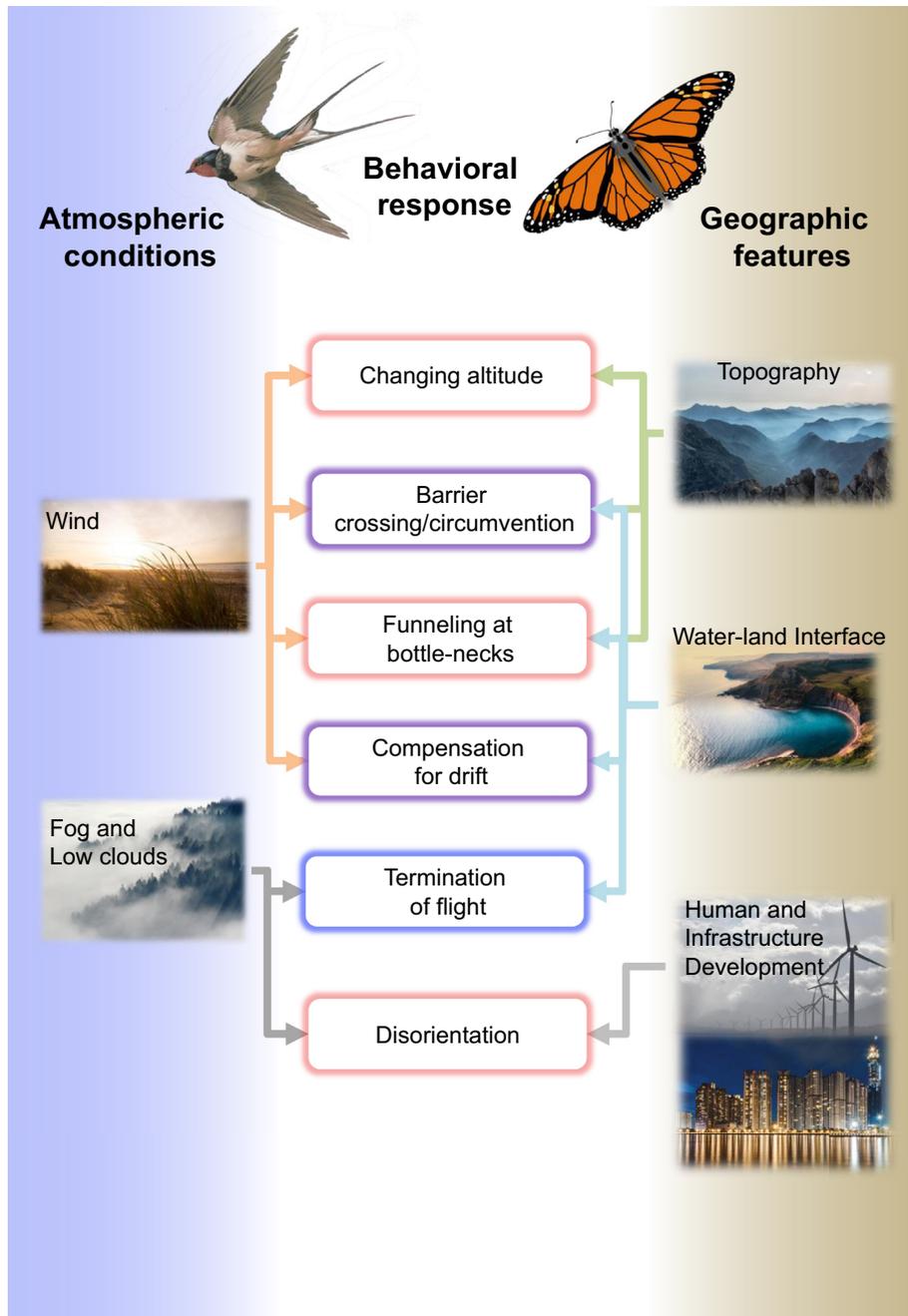
Figure 1. Major behavioral responses of flying migrants caused by the interaction between atmospheric conditions and geographic features as revealed by radar studies. Behavioral responses were found in insects only (blue glow), in birds only (red glow) or in both groups (violet glow). Birds changed their 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 Hoye 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 landbird 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).

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Ecography

Supplementary material

1 **APPENDIX**

2 **Details of the behavioral responses of migrants in relation to atmospheric conditions and geographic**

3 **features**

4

5 **1. Flight initiation, termination and migration intensity**

6 *Insects*

7   WIND: Radar studies have revealed that wind speed and direction have pronounced effects on

8 migratory departure and landing and consequently on the intensity of migration aloft (Rose et al. 1985,

9 Chapman et al. 2010, 2015a, Drake and Reynolds 2012). Favorable seasonal tailwinds (e.g. northerlies in

10 autumn) are associated with high migration intensity of many insects over the southern UK (Hu et al.

11 2016). Specifically, seasonally advantageous high-altitude tailwinds promote the initiation and

12 maintenance of migratory flight of autumn generation of the noctuid moth *Autographa gamma* heading

13 south, from northern Europe to the wintering grounds around the Mediterranean Sea (Chapman et al. 2008,

14 2015b). Airflows associated with synoptic scale fronts can provide short term 'windows' for crucial,

15 seasonally-adaptive movements in directions different from those in which the prevailing wind direction

16 would take the migrants. For example, massive autumn insect migration was associated with the passage

17 of synoptic-scale cold fronts, with insects flying in northerly winds immediately behind the leading edge

18 of the front (e.g., Beerwinkle et al. 1994, Feng et al. 2009, Chapman et al. 2010). Drake et al. (1981)

19 recorded spring movements of moths from the Australian mainland into Tasmania on warm northerly

20 (anticyclonic) airflows *ahead* of an approaching cold front. These rapid seasonal migrations may account

21 for large fluxes of insect biomass (Hu et al. 2016). Additionally, insects are often caught in the outflow

22 boundaries of convective storms (e.g., Achtemeier 1991, Browning et al. 2011) that may disperse insects

23 over long distances (e.g. Wilson and Schreiber 1986) and may also be trapped in the 'eye' or the rear of

24 hurricanes and typhoons (Van den Broeke 2013, Ma et al. 2018).

25   PRECIPITATION, CLOUDS AND FOG: Responses to, and effects of, rain on insect migration

26 are complex (Drake and Reynolds 2012, Reynolds et al. 2018). In temperate areas, rainy weather may

27 inhibit insect flight because of the associated lower air temperatures (and/or the cessation of convection in

28 the case of small day-flying insects, Russell 1999), and heavy, widespread rainfall inhibits insect flight

29 initiation and induces its termination (Drake and Reynolds 2012, but see Drake et al. 1981). Interestingly,

30 a sudden increase in nocturnal dragonfly migration over the Bohai Sea in northern China coincided with

31 foggy weather (Feng et al. 2006). Probably the flight of this diurnal migrant *Pantala flavescens* were

32 extended after dark because the insects found themselves over the sea, and the foggy conditions commonly

33 associated with the migration events might have also interfered with visual detection of ground features

34 (e.g. the coastline), which might otherwise have promoted landing (Feng et al. 2006). This could be because

35 fog is usually associated with relatively calm conditions at the surface, as indeed found in these heavy-

36 migration nights. The migrants were probably flying above the fog and likely departed for their journey at

37 dusk before the fog formed.

38   TEMPERATURE AND THERMAL UPDRAFTS: Because insects are poikilotherms, temperature

39 requirements for take-off and maintenance of flight must be satisfied first (Chapter 9 in Drake and

40 Reynolds 2012). Consequently, insects usually have a threshold temperature below which flight cannot be

41 initiated and/or maintained (e.g., Dudley 2000, Drake and Reynolds 2012). Temperature thresholds are

42 highly variable depending on the species, but various radar studies report that insects are usually detected

43 only when surface temperatures exceed 10°C (Wilson et al. 1994, Chapter 15 in Drake and Reynolds 2012),

44 likely representing an approximate threshold temperature for flight initiation in insects. In autumn, falling

45 temperatures promote the initiation of migratory flights in red admiral butterfly (Mikkola 2003), thus

46 increasing the probability of windborne transport on cool northerlies. Although some butterflies use soaring

47 flight (e.g., Gibo and Pallett 1979), we are not aware of any radar studies that explored it.

48   TOPOGRAPHY: To the best of our knowledge there are no radar studies on direct effects of

49 topography on flight initiation and/or termination of insect migration, largely because insect echoes on

50 scanning radars at low altitudes are swamped by much stronger 'clutter' echoes from ground features in

51 mountainous areas. However, entomological vertical-looking or tracking radars are generally less affected

52   by ground clutter and may thus be applied in the future to address questions related to the effects of

53   topography on migratory departure and termination.

54   WATER-LAND INTERFACE: Usually, nocturnal insect migration is largely halted by the onset

55   of dawn (Drake and Reynolds 2012). Yet, this termination of migratory movement is overridden if insect

56   migrants find themselves over water. Accordingly, the range of insect movement under these

57   circumstances may be considerably extended (Drake et al. 1981, Feng et al. 2009).

58   HUMAN AND INFRASTRUCTURE DEVELOPMENT: There are some incidental radar

59   observations of concentrations of insects around lights of large towns (e.g. Wad Madani in Sudan, see p.

60   275 in Drake and Reynolds 2012) and additional studies reported the attraction of large numbers of radar-

61   observed insect migrants to light traps following their descent from an overflying layer concentration and

62   subsequent flight near the ground near the trap (Reynolds and Riley 1988, Drake and Reynolds 2012, see

63   also Muirhead-Thompson 1991).

64

65   *Birds*

66   WIND: There is a balance between several endogenous and exogenous factors making up a bird's

67   decision to take off, and these include the bird's body condition, the quality of the resting site and the

68   meteorological conditions. Radar data showed that birds migrating selectively during nights with favorable

69   wind conditions speed up their flight by 30% (on average) compared to those disregarding the wind (Liechti

70   and Bruderer 1998), with likely implications for energy conservation (Pennycuick 1978, Alerstam 1991).

71   Several radar studies reported that flapping birds, such as waders, woodpigeons, starlings and geese, select

72   tailwinds to initiate their migration (e.g. Richardson and Haight 1970, Alerstam and and Ulfstrand 1974,

73   Green 2004). Migrating geese are selective in their choice of migration days and waders were found to

74   migrate in days with strong tailwinds that may even exceed the birds' own airspeeds (Green 2004).

75   Synoptic patterns of bird migration are structured by the presence of cyclones and anticyclones at

76   temperate latitudes, both in horizontal and altitudinal dimensions (Richardson 1978a, 1990). Early radar

77   studies in North America (Nisbet and Drury 1968, Richardson and Haight 1970, Richardson 1971,

78   Richardson and Gunn 1971) and Switzerland (Bruderer 1971) indicated that substantial spring migrations

79   initiate and continue under the light variable winds and fair weather that are typical near the centers of

80   high-pressure areas and in southerlies (spring migration tailwinds). Strong autumn migration occurs in the

81   eastern and central parts of high-pressure areas shortly after the passage of cold fronts in North America

82   (Richardson and Gunn 1971, Able 1972, Richardson 1972), Europe (Williamson 1969, Alerstam et al.

83   1973, Nilsson et al. 2019) and China (Mao 1985, Williams 1986), in light winds and strong northerlies

84   (autumn migration tailwinds).

85   In some cases, departure decisions could be fatal. Historical data from weather radar and water-

86   and land-based weather stations enabled Diehl et al. (2014) to reconstruct the circumstances leading to

87   mass bird mortality documented along the shores of Lake Michigan in northeastern Illinois in May 1996.

88   Storms that included strong winds, as well as heavy rain and hail, pushed birds over the lake and led to the

89   documented death of almost 3000 migratory birds from 114 species, mostly small passerines whose

90   carcasses were found in the lake's shores, with the actual numbers of dead birds likely much higher.

91   PRECIPITATION, CLOUDS AND FOG: Rain and precipitation, in general, are known to

92   suppress migratory flight (Richardson 1978a, 1990), but one must note that radars are unable to detect

93   birds that are flying under heavy rain. Also, fog may affect migration timing because migrating birds may

94   postpone their departure when visibility is poor (Alerstam 1990, Richardson 1990, Panuccio et al. 2019).

95   TEMPERATURE AND THERMAL UPDRAFTS: There is a strong relationship between rising

96   temperature and high migration intensity in spring (dropping temperature in autumn), as well as the

97   likelihood of flight initiation (Richardson 1978a, 1990). Temperature is the most important predictor of

98   spring migration timing and intensity based on data from a weather radar network deployed across North

99   America (Van Doren and Horton 2018). The same study also discriminated the effects of wind and

100 temperature: in similar wind conditions, more birds took flight when temperatures were warmer. Soaring

101 birds exploit thermal updrafts forming in the boundary layer during the day and initiate their flight when

102 thermals start developing, after dawn. Conversely, their flight terminates when no strong thermal are

103 available, after sunset (Spaar and Bruderer 1996, 1997).

104   TOPOGRAPHY: Radar studies have so far not found effects of mountain barriers on initiation or

105   termination of bird migration. Generally, birds tend to avoid high terrain elevations, as migration intensities

106   over mountains are substantially lower (sometimes by as much as 90%) compared to those over lowlands

107   (the Alps: Bruderer 1978, Liechti et al. 1996b, Aurbach et al. 2018; the Appalachians: Williams et al. 2001;

108   the Galilee in Northern Israel: Liechti et al. 2019). This 'funneling effect' described by higher bird

109   migration densities within the lowlands compared to low migration intensities over mountains, shows that

110   local topography may strongly influence migration patterns and can lead to local concentration of migrants

111   (Bruderer and Liechti 1990, Liechti et al. 1996b).

112   WATER-LAND INTERFACE: Land birds likely decide whether to stop, follow the coast or cross

113   the sea by considering the possible fatal consequences of drifting over the sea (Alerstam and Pettersson

114   1977, Horton et al. 2016). Bird decisions are related to the geographic settings (e.g., the width of the

115   crossing and coastline direction in relation to goal direction), as well as the specific wind conditions at the

116   crossing point. Several radar studies found no, or only weak, coastline effects on landing decision during

117   autumn and spring migration (Bruderer and Liechti 1998, Zehnder et al. 2001, Nilsson et al. 2014). One

118   explanation could be a progressive change of flight heading throughout the night, with an increasing rate

119   of migration towards land during the second part of the night, presumably due to the birds' preference to

120   stop-over and cease cross-country flight during the day (Alfia 1995, Bruderer and Liechti 1998, Horton et

121   al. 2016; see also Diehl et al. 2003). Radar observations have revealed that the peak longitude of arrival at

122   the coast for birds migrating aloft is related to the annual variability in the average wind speed and direction

123   over the Gulf of Mexico (Gauthreaux et al. 2006). Moreover, the average wind speed and direction over

124   the Gulf of Mexico affected also longitudinal patterns in the distribution of birds leaving stopover sites

125   along the coast during spring (Lafleur et al. 2016). Furthermore, nocturnally-migrating birds that were

126   found over the Great Lakes of North America at dawn were observed to gain altitude until seeing the closest

127   shoreline in their vicinity to which they reoriented rather than continued their cross-water journeys, leading

128   to greater densities of birds stopping-over near the shore (Archibald et al. 2017).

129   HUMAN AND INFRASTRUCTURE DEVELOPMENT: Although artificial light at night

130   associated with human development has been known to influence migrating birds during flight for

131   hundreds of years (Gauthreaux and Belser 2006), the response of birds to artificial light when initiating or

132   terminating migratory flight is not well understood. Recent weather radar studies have revealed that

133   migrating land birds stop-over in relatively high densities in city parks (Buler and Dawson 2014) and nearer

134   to highly light-polluted areas (McLaren et al. 2018). This broad extent stopover pattern may be caused by

135   young migrants orienting towards the skyglow of cities (Gauthreaux 1982) while selecting landing sites at

136   the termination of migratory flight. Estimating fine-scale temporal differences in departure timing is

137   possible with weather radar (Buler et al. 2018), revealing the influence of human development on migratory

138   flight initiation at a scale beyond the individual.

139

140   **2. In-flight behavior: speed, direction and altitude**

141   *Insects*

142   WIND: The optimal response of a flapping migrant to tailwinds is airspeed reduction, to decrease

143   the metabolic cost of flight. Higher airspeed is expected in headwind conditions (Pennycuick 1978). The

144   response of insects to wind conditions is strongly constrained by their lower airspeeds (Schaefer 1976,

145   Larkin 1991), which is virtually negligible in small insects. Migrating insects experiencing crosswinds

146   show a variety of responses, including complete and partial drift, as well as complete compensation for

147   lateral displacement in light winds (Chapman et al. 2010, 2015a,b, Reynolds et al. 2016). Preference for a

148   specific altitude was found to relate to strong wind support (Drake 1985, Wood et al. 2006, Drake and

149   Reynolds 2012). For instance, red admiral butterflies *Vanessa atalanta* chose cool northerly tailwinds for

150   their southern migrations from Scandinavia. They furthermore fly at high altitudes when strong winds from

151   the north predominate, but descend lower down when migrating in headwinds (Mikkola 2003).

152   Long-distance insect movements are typical in steady flows caused by the global-scale wind

153   patterns and the synoptic weather systems embedded within them, for example, the depressions and

154   anticyclones within the mid-latitude westerlies. Synoptic-scale winds (that are usually associated with

specific air temperature and precipitation conditions) may facilitate or impede insect migration. For example, the seasonal insect invasions of higher latitudes in spring often occur during spells of warm southerlies (northerlies in the southern hemisphere) on the western flank side of an anticyclone (Drake and Reynolds 2012).

PRECIPITATION, CLOUDS AND FOG: In the case of convective rain, insect migration can continue outside the precipitating cumulonimbus cells (Leskinen et al. 2011, Browning et al. 2011, Drake and Reynolds 2012). Browning et al. (2011) found that insects entrained in layers of warm air flowing into a thunderstorm took no action until they were within a 10-min period before the arrival of the storm's precipitation. They then descended with a tumbling motion – presumably an 'emergency' reaction to avoid being taken up to great altitude (and killed) in the violent updrafts associated with the storm. On several occasions, during nocturnal migration over the Bass Strait in Australia, flying moths were seen to be unaffected by the passage of a rain shower, suggesting that rain do not have any significant effect on their migration, at least if the insects are already airborne when the rain arrives, and the rain is not very heavy (Drake et al. 1981). Heavy, widespread rainfall induces descent that may result in landing and the termination of migration (Drake and Reynolds 2012; see also above).

TEMPERATURE AND THERMAL UPDRAFTS: Unlike the effects of temperature on flight initiation (see above Section 1.), radar evidence suggests that, once aloft, some large insects may fly in surprisingly low air temperatures (~5° C) (e.g. Drake and Reynolds 2012), presumably because they generate enough internal heat through their wing-beating action. Interestingly, dragonflies, butterflies and locusts concentrate in the boundaries of convective thermal cells (Schaefer 1976, Drake and Reynolds 2012), thus exhibiting a surprisingly convergent flight behavior with that of large soaring birds (Box 3, but see Geerts and Miao 2005).

TOPOGRAPHY: Insects were found to concentrate and respond to lee waves, topographic wind eddies and rotors (Chapter 11 in Drake and Reynolds 2012). Additionally, quasi-stationary convergence lines associated with rotors may provide aerial concentrating mechanisms and lead to high-density outbreaks of, for example, the African armyworm (*Spodoptera exempta*) (Rose et al. 2000). No radar study

181   has documented the seasonal near-ground passage of hordes of insects (such as butterflies and hoverflies,

182   Diptera: Syrphidae) through high mountain passes in the Pyrenees and Alps (e.g. Lack and Lack 1951,

183   Aubert et al. 1976).

184   WATER-LAND INTERFACE: Data from meteorological radars suggest a predisposition of

185   insects to resist being carried over coastlines and over the sea (Russell and Wilson 1996, 2001; see also

186   Chapman et al. 2010, 2015a, as well as Shashar et al. 2005). Nonetheless, radars have documented large-

187   scale insect migrations across the sea (e.g. Drake et al. 1981, Feng et al. 2006, 2009).

188   HUMAN AND INFRASTRUCTURE DEVELOPMENT: Despite the well-known attraction of

189   many insects towards artificial lights (the basis of the light-trap), radar detected insects engaged in steady

190   nocturnal migration at altitude do not appear to be affected by lights on the ground (see p. 276 in Drake

191   and Reynolds 2012). The powerful vertical-beam searchlight trap used in some Chinese radar studies (Feng

192   et al. 2009) constitutes an exception, but lights of this sort would rarely be encountered by migrating

193   insects.

194

195   *Birds*

196   WIND: Radar studies reveal the flight strategies of birds when facing various wind conditions.

197   Like in insects, the optimal expected response of a bird flying in tailwinds is airspeed reduction, and

198   airspeed increase in headwinds (Pennycuick 1978). This expectation has been empirically demonstrated in

199   a number of radar studies involving terrestrial flapping birds (Bloch and Bruderer 1982, Williams et al.

200   1986, Gudmundsson et al. 1992, Hedenström et al. 2002), terrestrial soaring-gliding birds (Spaar and

201   Bruderer 1996, 1997, Malmiga et al. 2014, Becciu et al. 2018) and seabirds employing a range of flight

202   modes (Mateos-Rodríguez and Bruderer 2012), with the exception of flapping auks whose response is

203   probably limited by their high wing loading.

204   Migrating birds in crosswinds demonstrate a wide range of strategies involving complete drift, as

205   well as partial and complete compensation for lateral displacement (Green 2001). A radar study in the

206   Strait of Gibraltar found that flapping seabirds (auks, puffins, gannets and small shearwaters) compensate

207 for wind drift independently of the predominant wind direction, unlike the larger shearwater species that

208 use a dynamic directional response to wind, allowing to be drifted in spring when westerly tailwinds are

209 prevalent and compensating for wind drift in autumn, when both easterly and westerly winds are similarly

210 frequent (Mateos-Rodríguez 2009).

211   To reduce metabolic costs of flight and increase ground speed, flying birds may adjust their flight

212 altitude to better exploit tailwinds along their predominant migratory direction. This has been suggested

213 for broad-front nocturnal migrants over Europe and Israel (Bruderer and Liechti 1995, Dokter et al. 2011),

214 as well as for migrating geese over southern Sweden (Green 2004). Diurnal migrating birds that use

215 flapping flight do not explore the entire air column of potential flight altitudes, but instead follow a rule of

216 climbing if tailwind assistance increases (Mateos-Rodríguez and Liechti 2012, Kemp et al. 2013). On the

217 other hand, nocturnal migrants reach higher altitude taking advantage of vertical wind shear, which arises

218 in particular synoptic situations related to the magnitude and direction of large-scale horizontal temperature

219 gradients (Dokter et al. 2013). Flight altitude in soaring migrants depends mainly on thermal conditions

220 (see below).

221   PRECIPITATION, CLOUDS AND FOG: Fog and low clouds limit bird visibility during flight

222 and may disrupt bird orientation (Lack 1962, Alerstam 1990, Richardson 1990). Radar-tracked Sandhill

223 cranes (*Grus canadensis*) showed more circuitous flight on a foggy day than on days with good visibility

224 (Kirsch et al. 2015; see also Pastorino et al. 2017). Precipitation, low clouds and fog have a strong influence

225 on visibility and obstacle avoidance behavior over complex terrain (Emlen and Demong 1978, Rüsch and

226 Bruderer 1981). For instance, when visibility is reduced, flight directions are more dispersed (Emlen and

227 Demong 1978, Liechti 1986, Becciu et al. 2017).

228   TEMPERATURE AND THERMAL UPDRAFTS: Birds are much more flexible than insects in

229 terms of timing and altitude of flight and may tolerate a wider temperature range. Nevertheless, radar-

230 based studies found that migrating raptors, as well as other soaring birds, increase their ground speed and

231 flight altitude in the hottest hours of the day – at midday and in the afternoon – probably because of the

232 stronger thermal uplift associated with high temperatures (Spaar and Bruderer 1996, Leshem and Yom-

233   Tov 1998). In fact, for soaring birds, flight altitude depends on the strength of thermal uplifts and on the

234   bird's decision to leave an uplift and start gliding (Pennycuick et al. 1979, Kerlinger et al. 1985, Horvitz

235   et al. 2014).

236   TOPOGRAPHY: Radar studies found that birds adjust their flight path with respect to mountain

237   ranges (Rüsch and Bruderer 1981, Liechti 1986, but see Mabee et al. 2006), suggesting that topographic

238   features constitute serious obstacles that animals have to cope with during migration (Bruderer 1978,

239   Liechti et al. 1995, Liechti et al. 1996a, 1996b). Birds were observed to deviate from their regular flight

240   direction to follow local topography through mountain passes (Williams et al. 2001). Nonetheless,

241   Hilgerloh et al. (1992) suggest that the Pyrenees do not constitute an ecological barrier to avian migrants

242   that commonly cross the ridge and similarly, another radar study found no effect of the Allegheny Front

243   ridgeline on autumn nocturnal migrants in West Virginia, USA (Mabee et al. 2006).

244   Weather conditions, such as wind were found to modulate the tendency of low-flying birds to

245   circumvent mountains instead of crossing them (Williams et al. 2001). For instance, circumvention

246   behavior of a complex and rough terrain is more pronounced under headwind conditions when most birds

247   fly at relatively low altitudes (Liechti 1986). On the other hand, under tailwinds birds are prone to cross

248   the Pyrenees in higher numbers (Lack and Lack 1951). Soaring migrants likely exploit orographic uplifts

249   while travelling along mountain ridges (Panuccio et al. 2016). Increasing migration intensity was observed

250   along the Appalachian Mountains that are orientated similar to the birds' main migration direction (Mabee

251   et al. 2006), likely indicating a funneling effect of the mountains. We note that high resolution wind flow

252   description and simulation of movement over complex terrain could provide deeper understanding of the

253   environmental factors faced by travelling birds (see Aurbach et al. 2018).

254   WATER LAND INTERFACE: Metabolic costs associated with flapping flight scale

255   disproportionately high in relation to body mass (Hedenström 1993). Since flapping is the flight mode used

256   by sea-crossing migrants including those which usually soar during flight, a negative relationship between

257   bird size and its sea crossing propensity has been documented in several radar studies. While small raptors

258   routinely cross the sea using flapping flight, likely because of their relatively low flapping flight metabolic

259   costs, larger soaring birds avoid sea crossing as much as possible (Meyer et al. 2000, 2003, Malmiga et al.

260   2014). While doing so, soaring birds tend to take long detours over land (Meyer et al. 2000, Alerstam

261   2001), concentrating in peninsulas, isthmuses and narrow land corridors (Nilsson et al. 2014). Furthermore,

262   the response of migrating raptors to wind conditions is modulated by the geography of their migration

263   route in Southern Italy, with an asymmetric behavioral response of the birds to crosswinds, compensating

264   when winds blew towards the sea and drifting when winds blew towards land (Becciu et al. 2018). Likely

265   the route selection was dependent on wind direction as migration intensity unexpectedly decreased with

266   increasing tailwind assistance, probably because tailwind conditions facilitate a shortcut of the birds over

267   the sea instead of undertaking a long over-land detour (Becciu et al. 2018). A recent broader-scale radar

268   study demonstrated a similar asymmetric response of nocturnally migrating songbirds to crosswinds near

269   the North American Atlantic coast in which the birds drifted when flying over inland areas, but

270   compensated for drift to avoid flying over the ocean near the coast (Horton et al. 2016). Noteworthy, when

271   migrating passerines found themselves offshore at dawn in unfavorable winds for a long overwater flight,

272   they reoriented toward land (Richardson 1978b).

273   Seabirds usually migrate across open waters without apparent barriers to their movements. Under

274   special conditions, such as those experienced when crossing a strait, seabirds may benefit from coastal

275   orographic features during flight, but their response may vary depending on their flight modes. Under

276   moderate winds and whenever visual contact with the coastline is present (as in the case of the Strait of

277   Gibraltar) seabirds changed their course, presumably to better respond to wind conditions. They

278   approached the coast under headwinds proportionally to the magnitude of wind intensity, as a strategy to

279   reduce the effect of headwinds and tended to fly further from the coast under tailwind conditions, to profit

280   from increasing tailwind speed there (Mateos-Rodríguez and Arroyo 2011).

281   HUMAN AND INFRASTRUCTURE DEVELOPMENT: On-the-ground anthropogenic

282   development has consequences on birds engaged in active migration, and radars have been widely used to

283   study the effect of wind turbines and, more recently, light pollution on the movement of migrating birds.

284   Radars provided insight of flight directions, altitudes and speeds of nocturnal migrants near wind turbine

11

285 facilities (e.g. Mabee et al. 2006, Cabrera-Cruz et al. 2017), with a recent suggestion that bird mortality

286 due to collision with wind turbines occurs regardless of the intensity of the migratory flow (Aschwanden

287 et al. 2018). Radar also assisted assessing the reaction of diurnally migrating birds to wind farms. For

288 example, geese and ducks migrating through the Baltic Sea (Desholm and Kahlert 2005) and raptors and

289 other soaring birds migrating through the Isthmus of Tehuantepec in southern Mexico (Villegas-Patraca et

290 al. 2014, Cabrera-Cruz and Villegas-Patraca 2016) seem to avoid entering newly installed wind farms and

291 change their track accordingly. Artificial lights also disrupt the flight of migrating birds (Cabrera-Cruz et

292 al. 2018), particularly under poor weather and low visibility conditions. For example, nocturnal migrants

293 circled around the steady burning lights of a communication tower during nights with low cloud elevation

294 as opposed to migrants' linear trajectories when no such conditions prevailed (Larkin and Frase 1988).

295 However, if the source of light is bright enough, lights will affect the flight behavior of migrating birds

296 regardless of the weather conditions. For example, Bruderer et al. (1999) demonstrated that nocturnal

297 migrants changed their flight direction by re-orienting themselves $8\pm10°$ away from a bright light source

298 pointed at them, and that this stimulus also made some birds to decrease their ground speed or change their

299 flight altitude. The drastic effect of the super bright beams of light used during the 9/11 "Tribute in Light"

300 memorial in New York city on nocturnal migrants include the massive bird attraction to the site when lights

301 were on. The birds flew in circles around the beams of light but nonetheless their concentration dissipated

302 and they resumed their normal migratory flight when the lights were turned off (Van Doren et al. 2017).

303 These findings are just a few examples of the extensive research conducted with radar technology which

304 can be used to inform conservation efforts. Hüppop et al. (2019) provide an in-depth review of radar

305 applications to biological conservation of aerial vertebrates, including migratory birds.

306

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