ECOGRAPHY

Review and synthesis

Perspectives and challenges for the use of radar in biological conservation

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Ecography
42: 1–19, 2018
doi: 10.1111/ecog.04063

Subject Editor:
Judy Shamoun-Baranes
Editor-in-Chief: Miguel Araújo
Accepted 5 December 2018

Radar is at the forefront for the study of broad-scale aerial movements of birds, bats and insects and related issues in biological conservation. Radar techniques are especially useful for investigating species which fly at high altitudes, in darkness, or which are too small for applying electronic tags. Here, we present an overview of radar applications in biological conservation and highlight its future possibilities. Depending on the type of radar, information can be gathered on local- to continental-scale movements of airborne organisms and their behaviour. Such data can quantify flyway usage, biomass and nutrient transport (bioflow), population sizes, dynamics and distributions, times and dimensions of movements, areas and times of mass emergence and swarming, habitat use and activity ranges. Radar also captures behavioural responses to anthropogenic disturbances, artificial light and man-made structures. Weather surveillance and other long-range radar networks allow spatially broad overviews of important stopover areas, songbird mass roosts and emergences from bat caves. Mobile radars, including repurposed marine radars and commercially dedicated 'bird radars', offer the ability to track and monitor the local movements of individuals or groups of flying animals. Harmonic radar techniques have been used for tracking short-range movements of insects and other small animals of conservation interest. However, a major challenge in aeroecology is determining the taxonomic identity of the targets, which often requires ancillary data obtained from other methods. Radar data have become a global source of information on ecosystem structure, composition, services and function and will play an increasing role in the monitoring and conservation of flying animals and threatened habitats worldwide.

Keywords: radar, aeroecology, insects, birds, biological conservation, phenology

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Introduction

For many organisms, the airspace provides habitat for a significant part of their lives. It is essential for foraging, commuting, and migration. The 'airspace' in question here primarily concerns the lower parts of the troposphere where an organism's presence indicates use of some airborne resource, from flying insects as food to favourable winds aloft supporting movement (Diehl 2013). It is habitat for incredible numbers of microorganisms, wind dispersed seeds and fungal spores, arthropods, bats, and birds (Kunz et al. 2008, Womack et al. 2010, Drake and Reynolds 2012, Diehl 2013, Davy et al. 2017, Reche et al. 2018). Hahn et al. (2009) calculated, for example, that some 2.1 billion songbirds and near-passerine birds migrate from Europe to Africa in autumn, and recently Dokter et al. (2018) estimated from radar data that 4.7 billion passerine-sized birds leave the USA southward in autumn and 3.55 billion birds return northward in spring. According to data from 70 European weather radar stations from northern Scandinavia to Portugal, nocturnal autumn migration averages on a broad scale to almost 400 birds km^{-1} h^{-1} Nilsson et al. (2019). The mass of insects in the air is even more impressive: Hu et al. (2016) quantified biomass flux over southern England for high-flying (>150 m) insects by radar and estimated that above this region alone about 3.5 trillion insects equaling 3200 tons of biomass migrate annually.

Our ability to understand the manner and magnitude of airspace use by animals, namely birds, bats, and insects is linked to our ability to detect individuals or groups in flight, and the same holds for related conservation issues. Flying animals are challenging study subjects, because they are often difficult to observe directly. By the 19th century, it became clear from observations at lighthouses and lightvessels that many diurnal bird species become nocturnal during migration (Gätke 1895, Barrington 1900, Clarke 1912, Munro 1924, Lewis 1927). Roughly two thirds of the European bird species migrate mainly or exclusively at night (Martin 1990). Many insects also migrate or otherwise move about the landscape at night (Chapman et al. 2015), and most bats are exclusively nocturnal. Moreover, the vast majority of aerial species are also small (Bridge et al. 2011), often fly at appreciable altitudes, and are transient. For example, more than a century ago, Gätke (1895) had noted of diurnal migrants 'that, as long as migration proceeds under its normal conditions' its 'elevation is, in the case of by far the larger number, so great as to be completely beyond the powers of human observation…'. With the introduction of radar by the military during the Second World War it soon became obvious that radar could help fill gaps in our understanding of how flying animals use the airspace (Brooks 1945, Lack and Varley 1945, Buss 1946, Sutter 1957, Eastwood 1967). Since that time, many different types of radar (Table 1) have been broadly applied to study the 'invisible parts' of the movements of both birds and insects on a broader scale, primarily in Europe, North America, east Asia and Australia (Lack 1959, Drury and Keith 1962, Alerstam 1972, Myres and Apps 1973, Williams and Ying 1990, Bruderer 1997a, b, 2003, Drake and Reynolds 2012, Beason et al. 2013, Drake and Bruderer 2017).

While there has been a rapid development of telemetry and other advanced tracking and data logging technologies to study the movements of individuals in detail (Stutchbury et al. 2009, Bridge et al. 2011, Kissling et al. 2014, O'Mara et al. 2014, Roeleke et al. 2016, Weller et al. 2016), radar is still at the forefront with regards to comprehensiveness and the spatial and temporal extent of its applicability to aeroecological research on bats, birds and insects. Furthermore, the majority of insect species, and the smallest bats and birds, currently fall below the size threshold for the application of other long-range tracking technologies. However, a major challenge in aeroecology is the ability to link radar data with species identification or with individual tracking information, which will allow observations of individuals to be used to infer population-level movements and processes. With the advent of large-scale tracking capabilities such as the Icarus Initiative (<https://icarusinitiative.org/>), which can track individually-tagged animals using the International Space Station, the combination of individual tracking and large-scale radar observations may soon be realised.

Although the contribution of radar technologies to our understanding of the biology of flying animals on a more local scale is well recognized, country- to continent-wide networks of digital weather surveillance radars (WSRs) in particular have proven to be a central technology to the study of aeroecology (Gauthreaux et al. 2003, Kelly et al. 2012, Shamoun-Baranes et al. 2014, Bauer et al. 2017, 2019, Dokter et al. 2018, Van Doren and Horton 2018). These radars offer an unparalleled opportunity for objective, continuous, reliable, cost-effective large-scale data collection of aerial animal movements, which can assist in delineating and managing conservation areas, migratory bottlenecks (i.e. points where geography constrains migration, leading to significant concentrations of populations; Bayly et al. 2017, Panuccio et al. 2018), population monitoring, pest control, and many other aspects of biological conservation. Furthermore, many types of smaller (and often relatively mobile) radars have broad applications in environmental impact studies and monitoring of cryptic species (Table 1).

Here, we provide an overview on past, current and expected future applications of radar in biological conservation. Specifically, we discuss the use of radar for 1) providing information on distribution, population sizes, dynamics and fluxes of flying animals, 2) the identification and management of conservation areas, and 3) the evaluation of effects of anthropogenic obstacles, artificial light and human disturbances on behaviour. We discuss how radar can be applied to issues relating to the conservation of biodiversity and ecosystems, highlight the challenges associated with its application and indicate areas ripe for further investigation. Regarding the huge number of articles and reports on the topic, we are aware that this review

Table 1. Examples of different types of radar and their suitability for investigating conservation related issues in aeroecology.

Radar type	Antenna type	Typical working range[1]	Operating networks	Target identification[2]	Individual tracks[3]	Height distribution	Horizontal distribution	Flight speed	Direction of movements	Attraction or avoidance behaviour	Quantification of numbers or biomass flux	Examples
Tracking radar	parabolic dish antenna in target tracking mode[3]	< 20 km	–	+++	+++	–	–	+++	++	+++	–	Konrad et al. (1968), Schaefer (1968), Vaughn (1985), Larkin and Frase (1988), Bruderer et al. (1995), Alerstam and Gudmundsson (1999)
Tracking or marine radar	rotating parabolic dish antenna (some with different elevations)	< 5 km	–	–	++	++	+	++	+++	++	++	Cooper et al. (1991), Gauthreaux (1991), Bruderer et al. (1995)
Tracking or marine radar	fixed parabolic dish	< 5 km	–	++	–	+++	–	–	+	+	+++	Schmaljohann et al. (2008), Bruderer et al. (2012), Hill et al. (2014)
Marine radar	horizontally rotating fan-beam	< 10 km	–	–	++	–	++	++	++	+	+	Harmata et al. (1999), Mabee and Cooper (2004), Desholm and Kahlert (2005), Hüppop et al. (2006), Fijn et al. (2012), Plonczkier and Simms (2012)
Marine radar	vertically rotating fan-beam	< 2 km vertically	–	–	+	++	–	–	–	+	+	Harmata et al. (1999), Mabee and Cooper (2004), Hüppop et al. (2006), Fijn et al. (2015)
Air-traffic surveillance radar	different types of rotating antenna from dish to stacked beam	< 10 to > 150 km	++	–	++	+[4]	+	++	+++	+	+	Sutter (1957), Lack (1959), Alerstam (1972), Buurma (1995), Ruhe (2000)
Air-traffic surveillance radar	nodding antenna	< 10 km	–	–	–	+++	–	–	–	–	+	Sutter (1957), Lack (1960)
Vertical-looking entomological radar	vertical beam, with rotating linear polarisation and narrow-angle conical scan	up to ~1100 m vertically	–	+	–	+++	–	–	++	–	+++	Chapman et al. (2003), Drake and Reynolds (2012)
Dedicated bird radar	solid state, phased array, x-band, 17 beams 0–60 deg[5]	< 15 km	–	–	+++	+++	+++	+++	+++	+++	+++	Robin Radar MAX system: <www.robinradar.com>, Drake and Bruderer (2017)

(Continued)

Table 1. Continued

Radar type	Antenna type	Typical working range[1]	Operating networks	Target identification[2]	Individual tracks[3]	Height distribution	Horizontal distribution	Flight speed	Direction of movements	Attraction or avoidance behaviour	Quantification of numbers or biomass flux	Examples
Weather radar	parabolic dish, rotating at different elevations	< 200 km	+++	–	–	+++	+++	++	++	+	+++	Gauthreaux (1992), Diehl et al. (2003), Gauthreaux et al. (2003), Buler et al. (2010, 2012), Dokter et al. (2011, 2018), Shamoun-Baranes et al. (2014)
Radar wind profiler	array of 5 upward looking antennas	< 4 km	+	–	–	+	–	–	+	–	++	Weisshaupt et al. (2017, 2018)
Scanning harmonic radar	two rotating parabolic dishes (transmitter and receiver)	< 1 km	–	+++[6]	+++	–	–	+++	+++	++	–	Drake and Reynolds (2012)
Portable harmonic direction-finders	small transmitter and receiver antennas or arrays	a few metres–50 m max	–	+++[6]	++	–	–	+++	+++	++	–	Drake and Reynolds (2012)

–: not possible, +: possible under certain conditions, ++: well suited, +++: excellent.
[1] The working range strongly depends on the characteristics of the targets (size/radar cross section; single animal or flock) and radar (wavelength, power).
[2] Taxonomic groups might be identified by their wing beat patterns, radar cross sections or polarimetric characters.
[3] In 'true' tracking radars circuits are activated that cause the antenna to follow a selected target automatically, while in radars with rotating antennas, trajectories are calculated by software from consecutive scans.
[4] This depends on the antenna type of the radar.
[5] There are several former commercial developments, mostly based on civil marine radar components, employing a variety of antenna types and scanning configurations (for technical details see Drake and Bruderer 2017).
[6] Insects are individually tagged with a transponder.

can by no means be comprehensive. Rather, it presents a representative selection of studies on the conservation aspects of aeroecology. However, we do not cover other applications of radar in biological conservation such as the remote sensing of habitat assessments and changes (Kuenzer et al. 2014, Howison et al. 2018), marine pollution (Fingas and Brown 2014, Toupouzelis et al. 2015), monitoring of marine mammals (DeProspo et al. 2005), tracking cryptic terrestrial vertebrates (e.g. frogs/toads, snakes), some of which are highly endangered (Engelstoft et al. 1999, Gourret et al. 2011, Aumann et al. 2013, Roznik and Alford 2015), and the detection of (illegal) fishing and whaling (Lee and Kim 2004, Doumbouya et al. 2017). Aspects of avian impacts on flight safety are also not covered here but have been treated comprehensively by van Gasteren et al. (2019).

Animal distribution, numbers and biomass in time and space

Many migrant species are extremely abundant and their seasonal migrations can significantly affect the communities that they pass through, affecting ecosystem function via mechanisms such as predation, herbivory and competition, while also transporting large amounts of nutrients, propagules, pathogens and parasites (Bauer and Hoye 2014, Hu et al. 2016, Bauer et al. 2017). Investigating the distribution and estimating numbers of nocturnal, small or high-flying animals can be very challenging, particularly in very mobile species or across larger spatial and temporal scales. Depending on the question, species, area or time scale, different types of radar can be used to address these issues (Table 1).

The first attempts to quantify nocturnal bird migration were made with short-range X-band scanning radar (Eastwood 1967, Drake and Bruderer 2017). In many countries, military and civil air traffic radar is used to study the spatial and temporal distribution of bird migration on a larger, often national scale (Sutter 1957, Lack 1959, Alerstam 1972, Buurma 1995, Ruhe 2000). However, continent-wide studies have only become possible via the use of data from WSRs. In WSRs, the focused beam of a parabolic antenna is swept azimuthally through a number of elevation angles yielding a three-dimensional coverage of the airspace over long ranges (hundreds of km) and can provide information about the horizontal and vertical distribution of organisms (Dokter et al. 2011, 2018, Stepanian et al. 2014, Chilson et al. 2017, Drake and Bruderer 2017). Today, networks of WSRs span much of the terrestrial landmass in many parts of the world (Fig. 1), enabling continental-scale analyses of animal movements, density, fluxes (i.e. the rates at which animals or biomass pass through a unit 'window' oriented at right-angles to their direction of movement), aerial flyways, and seasonal movement phenology (Gauthreaux et al. 2003, Kelly et al. 2012, 2016, 2017, Shamoun-Baranes et al. 2014, Dokter et al. 2018, Nilsson et al. 2019). In some cases, WSR measurements are archived in long-running databases, enabling analyses of population trends and persistence. The extensive research on target identification and measurement standards established for meteorological applications as well as huge data archives should ensure objective, intercomparable, long-term measurements across much of the globe (Chandrasekar et al. 2013, Stepanian et al. 2016). An example of such benefit is in detecting and monitoring large colonies of bats; a capability demonstrated for several North

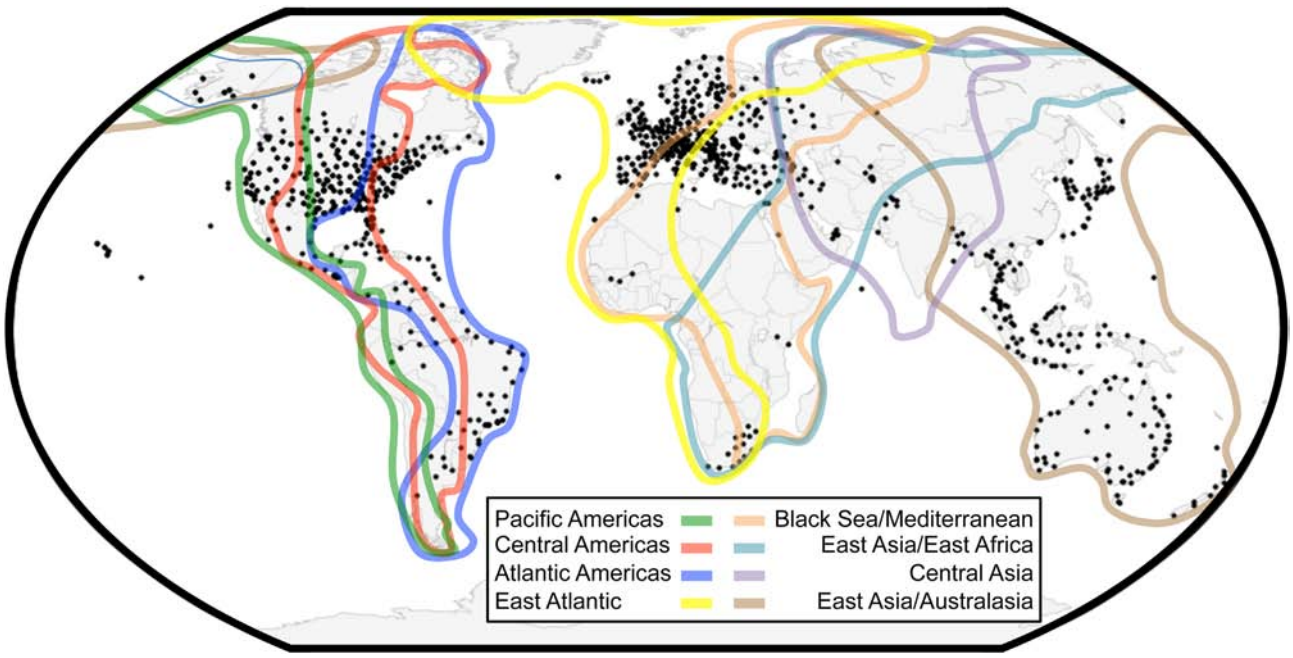

Figure 1. Global overview of weather radar sites registered with the World Meteorological Organization, with the major global flyways superimposed. Flyways were obtained from <www.birdlife.org/worldwide/programme-additional-info/migratory-birds-and-flyways>.

American bat colonies (Horn and Kunz 2008, Stepanian and Wainwright 2018) and readily transferred to other regions having radar infrastructure (Fig. 2). However, in most cases information on taxonomic identity needs to be derived from other methods such as visual, including night vision techniques, or acoustic observations (Horton et al. 2015, Molis et al. in press) or trapping.

By analyzing data from a WSR along the northern coast of the Gulf of Mexico, Gauthreaux (1992) noted a decline in the amount of trans-Gulf migration and changes in the migrants' seasonal timing compared with the mid 1960s. The percentage of days with trans-Gulf flights in the spring declined by almost 50% from 1965–1967 to 1987–1989. At that time WSR data were recorded and stored as films and analyses required a large amount of manual work (Gauthreaux 1992). Nowadays, the progress in WSR technology, namely the upgrade to dual-polarization operation, digital data storage facilities, sophisticated methods to classify targets and to extract information on animals from WSR data (Dokter et al. 2011, 2019, Chandrasekar et al. 2013, Stepanian et al. 2014, 2016, Chilson et al. 2017) allow a broad spectrum of analyses on spatial and temporal changes in numbers or biomass and phenology, e.g. under the influence of climate change (Kelly et al. 2016, 2017). For example, Stepanian and Wainwright (2018) found that spring migration and the summer reproductive cycle of Brazilian free-tailed bats *Tadarida brasiliensis* roosting in one of the largest aggregations of mammals on Earth (a cave in suburban San Antonio, Texas) have advanced by roughly two weeks over a 22 yr period. They also quantified the ongoing growth of a recently established overwintering population. On a local scale (i.e. less than a few kilometres) a spectrum of non-stationary radars have been used in relation to conservation issues which are difficult to investigate by other methods. Often, these were relatively inexpensive marine surveillance radars, either as off-the-shelf units or specially modified, e.g. by tilting the antenna from horizontal to vertical rotation or by substituting the original beam antenna by a parabolic dish antenna (Beason et al. 2013, Table 1).

Systematic studies to measure the migration traffic rate (i.e. the migration flux through a stationary counting plane) and later also the density of migration (i.e. the number of birds flying per unit volume) started in 1968 with the 'Superfledermaus' (Bruderer et al. 2012, Drake and Bruderer 2017). Later, many studies followed using either fixed or scanning beams and antennas of different shapes. A narrow, clearly defined pencil-beam is optimal for quantitative recording of migration traffic rate (MTR; Schmaljohann et al. 2008, Drake and Bruderer 2017), but attempts to quantify migration were also made with the standard beam antenna of marine or dedicated bird radars (Harmata et al. 1999, Hüppop et al. 2006, Bruderer et al. 2012, Beason et al. 2013, Fijn et al. 2015, Gürbüz et al. 2015, Gerringer et al. 2016, Urmy and Warren 2017, Walsh et al. 2017, Molis et al. in press).

Marine radar has also been used to monitor numbers and flight behaviour of threatened seabird species, such as petrels and shearwaters, terns, murrelets and other small auks as they move between breeding and feeding areas (Day and Cooper 1995, Cooper et al. 2001, Raphael et al. 2002, Day et al. 2003, Hamer et al. 2005, Cragg et al. 2016, Urmy and Warren 2017), often during the night or at dawn and dusk. In murrelets, counts by marine radar cover much larger areas compared to audio-visual surveys or autonomous acoustic recording, but radar identification of murrelets proved unreliable in winds exceeding 18 km h^{-1}: strong tail winds increased flight speeds of all birds and head winds reduced them; in either case, differentiating murrelets from slower flying birds became problematic (Cragg et al. 2016). Nonetheless, radar is capable of detecting population trends and providing information on habitat associations in areas

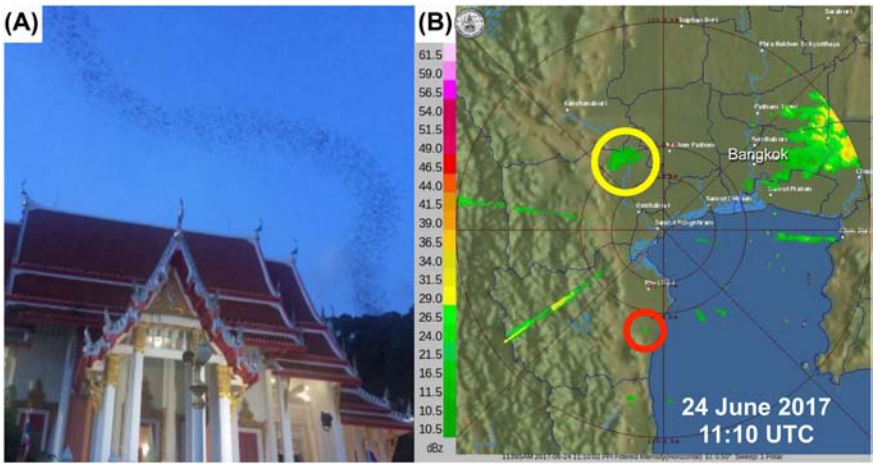

Figure 2. Weather surveillance radar as internationally-standardized infrastructure for wildlife monitoring. (A) An evening bat emergence from the cave colony at Wat Khao Chong Pran in Photharam, Thailand (photo courtesy of TripAdvisor). (B) An image of reflectivity factor from the Samut Songkhram radar site on 24 June 2017 at 11:10 UTC. Probable emergence signatures are identified at the Wat Khao Chong Pran bat cave (yellow) and Nanyang bat cave (red). Local sunset for this date was approximately 11:52 UTC.

where flight paths are confined by the landscape, such as fjords and valleys (Cragg et al. 2016).

Special-purpose entomological radar systems for observation and monitoring of insect migration (as opposed to foraging behaviour) were formerly mainly horizontal-scanning pencil-beam units, but since about the year 2000 these have been superseded by nutating vertical-beam systems which are much amenable to autonomous operation (Drake and Reynolds 2012, Drake 2016, Drake and Bruderer 2017, Drake and Wang 2018). Entomological radars provide various simple measures of the intensity of flight activity such as volume densities, or fluxes (Drake and Reynolds 2012, Reynolds et al. 2017). These measures can then be integrated to produce, respectively, estimates of area density (i.e. the number of targets above a unit area of the Earth's surface), and MTR (Drake and Reynolds 2012, chapter 9). Finally, estimates can be made of 'total overflights', and thus ecologically important bioflows, in particular directions, over periods from a few days or even over whole seasons (Hu et al. 2016), and very recently even on vertical fluxes (Drake and Wang 2018). Examples of area densities, traffic rates, and total overflights for insects are given in Drake and Reynolds (2012, chapter 10). While these estimates were primarily for pest species, Chapman et al. (2005) estimated migration rates for a natural enemy (a carabid beetle). Integrated measures of migration bioflow can be derived for other non-pest insects such as dragonflies (Feng et al. 2006) or species of conservation relevance, provided the focal species is distinguishable (by, for example, natural history, size, or shape) from other aerial fauna.

Customized entomological radars employing the nutating vertical-beam configuration supply useful information not only about an individual insect's flight trajectory, but also some indication as to its identity (Drake and Reynolds 2012, Drake 2016, Drake et al. 2017). Nonetheless, there are rather few of these special-purpose radars in operation, and so for regional and continent-wide monitoring of insects, including those of conservation interest, we need – as in birds – to utilise data from networks of Doppler WSRs (Shamoun-Baranes et al. 2014, Stepanian and Horton 2015, Stepanian et al. 2016). Doppler WSRs make use of the frequency shift of a returned radar signal to derive velocity data of remote objects. Except in Finland (Nieminen et al. 2000, Leskinen et al. 2011), only recently has Doppler WSR been used more routinely to monitor insect migration, and pest management applications guide much of that research (Ainslie and Jackson 2011, Rennie 2012, 2014, Westbrook et al. 2014, Boulanger et al. 2017). Applications to swarming species which temporarily dominate the airspace are obvious candidates to study e.g. the (non-migratory) nuptial and oviposition flights of mayflies (Ephemeroptera) above rivers and lakes (Drake and Reynolds 2012, chapter 14, and Fig. 3), which can be used as an indicator of water quality. There have also been reports of migrating monarch butterflies *Danaus plexippus* observed on WSR (Melnikov et al. 2014). However, these reports require further documentation as a major challenge remaining in radar aeroecology is determining the taxonomic identity of the observed targets. Generally, WSR monitoring of aerial insect populations will require ancillary information on species identity derived from other techniques, such as concomitant visual observations, trapping, or vertical-looking entomological radar described above.

In an ambitious study, Hu et al. (2016) estimated total seasonal migration, in terms of numbers and biomass, above southern England, using radar to quantify the high-flying large insect populations and trapping to quantify small insects, and insects flying at low altitudes. By these means they were able to quantify the total biomass (~3200 tons annually) and also to estimate the aerial transport of key nutrients such as nitrogen and phosphorous. Because the mass migrations of medium- and large-sized insects was generally northwards in spring and southwards in autumn, these bioflows represent net annual exchange of energy and nutrients into and out of southern England, with considerable impacts on the ecosystems utilized by the migrants. Although the aerial transport of insect biomass was surprisingly large (considering the cool maritime climate of the United Kingdom), it will no doubt be greatly exceeded in warmer regions of the world. However, the extent of animal migrants on nutrient transport across ecosystems will require additional information on known fates of the animals or nutrient deposition rates, derived from other methods, which can then be scaled up using the movement estimates derived from radar.

Identification and management of conservation areas

Many migratory bird species are in decline (Kirby et al. 2008, Wilcove and Wikelski 2008, Bairlein 2016). Conservation of migratory populations has increasingly focused on protection of key breeding, wintering and stop-over habitats, yet 91% of 1451 migratory bird species investigated by Runge et al. (2015) were inadequately supported by protected areas across their migratory cycle. This focus on key sites is most acute in the human-dominated landscape of Europe, where relatively small protected areas across nation-states are surrounded by highly urbanized habitats, intensively used farmland, or commercial forests.

Species conservation often focuses on the identification and protection of critical terrestrial or aquatic habitats. Applications of species conservation laws explicitly hinge on biologists' notions of habitat. Recent recognition that parts of the airspace may, at least temporarily, also represent important habitat for flying animals suggests the need to also identify airspaces critical to populations of flying animals and possibly establish aerial reserves. For example, traditional feeding or migratory flight corridors or airspaces proximal to large bat or bird roosts, may require preservation (no wind turbines, power lines, lit buildings or other man-made obstacles) or some other form of legal protection

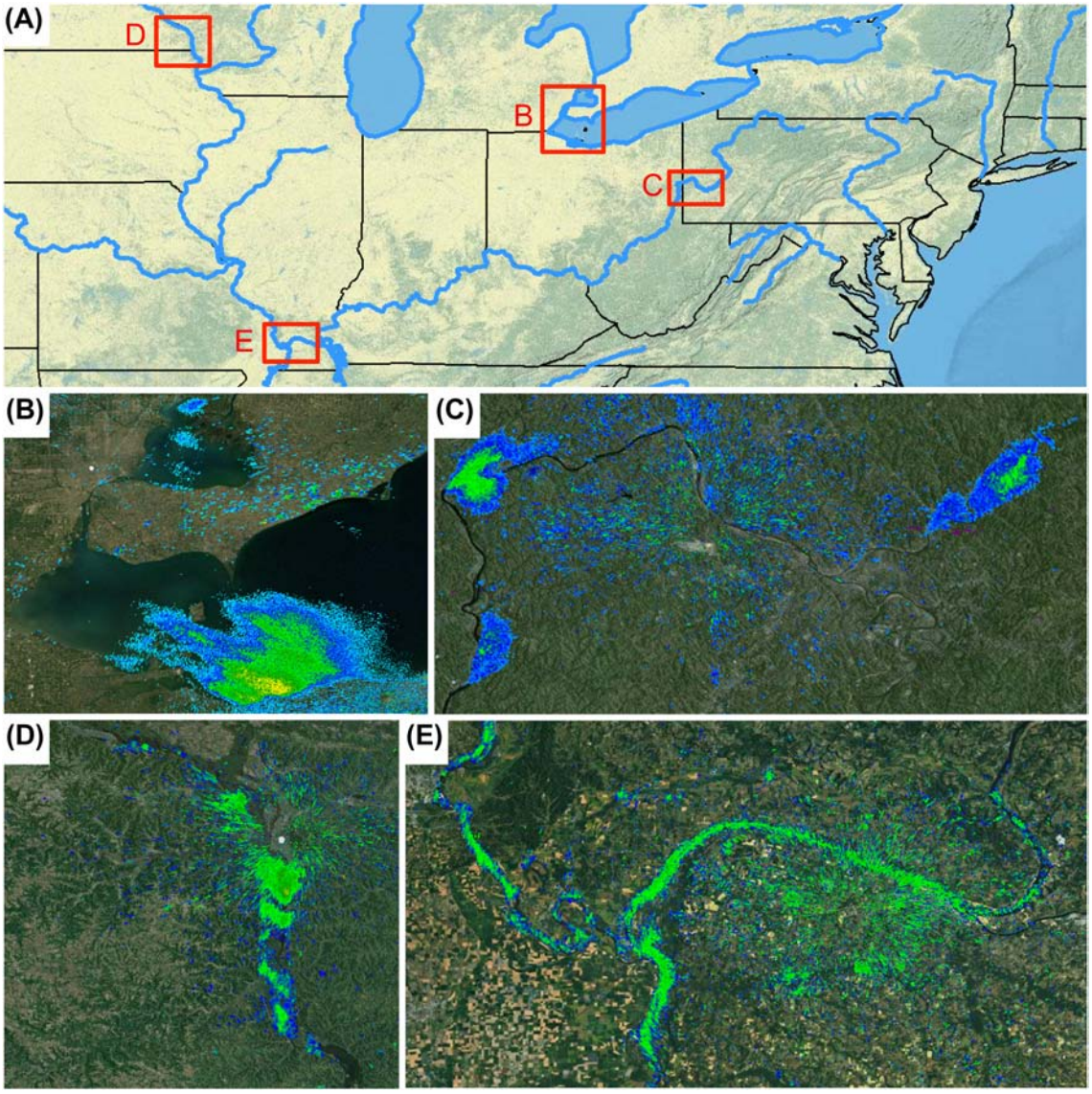

Figure 3. Radar as a tool for monitoring aquatic ecosystem health, phenology, and biomass production. (A) Major waterways of the northeastern and north-central United States. (B) Dusk emergence of giant mayflies *Hexagenia limbata* on Lake Erie and Lake St Clair as seen by the Detroit, Michigan and Cleveland, Ohio weather radars on 19 June 2017. (C) Dusk emergence of aquatic insects on the Allegheny and Ohio Rivers as seen by the Pittsburgh, Pennsylvania radar on 13 July 2017. (D) Dusk emergence of mayflies *Hexagenia bilineata* on the upper Mississippi River as seen by the La Crosse, Wisconsin radar on 11 July 2017. (E) Dusk emergence of aquatic insects on the Ohio and Mississippi Rivers as seen by the Paducah, Kentucky radar on 20 August 2017.

(Diehl 2013, Lambertucci et al. 2015, Diehl et al. 2018). Such reserves could benefit migratory birds and bats moving through geographic and seasonal bottlenecks (Rydell et al. 2014, Bayly et al. 2017, Panuccio et al. 2018, Sherry 2018) or more locally, roosting birds and bats or foraging waterfowl and raptors that use the same airspaces on a recurring basis. Airspace protection does not need to be absolute: dynamic aerial reserves would offer protection at critical points in the season and allow human use at other times (Davy et al. 2017). Radar-based detection of high concentrations of flying animals moving through a particular airspace could prove useful for identifying key areas of habitat and assist in delineating future aerial conservation areas. Currently, our ability to envision airspace reserves is ahead of our ability to actually identify airspaces that might be critical for species conservation. However, the legal and policy apparatus presumably necessary to establish aerial reserves is still unclear and in need of development (Davy et al. 2017). Furthermore, radar data can efficiently highlight key areas for the protection of aerial animals on the ground.

The challenges inherent in the conservation of migratory populations place considerable demands on the need to identify key habitats as part of a larger reserve network. Ideally, such networks would provide resources that sustain bird

populations while limiting the diversity and magnitude of threats (Kirby et al. 2008, Diehl 2013, Lambertucci et al. 2015, Bairlein 2016, Davy et al. 2017). Reserve-based conservation should also encompass all stages of the annual cycle (Martin et al. 2007, Runge et al. 2014, 2015) and therefore necessarily include areas covering large geographical ranges that often cross political boundaries (Wilcove and Wikelski 2008, Runge et al. 2014, Bairlein 2016). Among habitats used by migrating birds and bats throughout the annual cycle, we generally know least about what stopover and aerial habitats may be most important to species conservation, since use of these habitats is ephemeral and widespread. Meeting this challenge necessarily favors methods of identifying important habitats that are efficient, cost effective, and operational across large spatial scales and over long timescales (Martin et al. 2007, Runge et al. 2014).

WSR networks match the spatial extent and comprehensiveness of the habitats used by birds during continental migration (Fig. 1) and thus have application for monitoring migratory behaviour along entire sections of a flyway (Kelly et al. 2012, Shamoun-Baranes et al. 2014, Bauer et al. 2017, Dokter et al. 2018, Van Doren and Horton 2018, Nilsson et al. 2019). At local or regional scales, WSR has effectively been used to identify important stopover sites for migratory birds (Diehl et al. 2003, Buler and Moore 2011, Ruth et al. 2012, Buler and Dawson 2014, and Fig. 4), wintering sites for waterfowl (Buler et al. 2012), and key roost sites for birds (e.g. purple martins *Progne subis*; Russell and Gauthreaux 1998, Russell et al. 1998, Bridge et al. 2016) and bats (Horn and Kunz 2008, Stepanian and Wainwright 2018). Given the high risk to many key stopover sites for threatened migratory species globally (for example tidal mudflats along the Yellow Sea; Studds et al. 2017), radar will play an increasingly important role in assessing the value of these areas for the species they support. WSRs, along with other radar methods may also quantify bird and bat movements in ways that identify airspaces important to species conservation but are also reliant on supporting methodologies to elucidate species composition (Diehl et al. 2018).

Effects of disturbance, artificial light and anthropogenic obstacles on behaviour

Human activities can have serious negative consequences on wildlife, especially in sensitive conservation-relevant species or in densely populated urban and suburban landscapes where interactions can lead to conflicts. For example, around the world, fireworks are used to celebrate special occasions, but these displays can cause widespread disturbance in birds (Shamoun-Baranes et al. 2011, <http://horizon.science.uva.nl/fireworks/> and Fig. 5). Since they normally happen at night, the evaluation of the effects on wildlife on a large scale is difficult (Stickroth 2015). By means of an airport surveillance radar, Jänicke and Stork (1979) investigated the effects of fireworks on roosting flights of crows wintering in and around Berlin, Germany. While huge numbers normally flew over the city to their night roost close to the airport, they avoided this on New Year's Eve and instead flew to other roosting sites some 10 to 15 km further east. Shamoun-Baranes et al. (2011) quantified the reaction of birds to New Year's Eve fireworks in the Netherlands in three consecutive

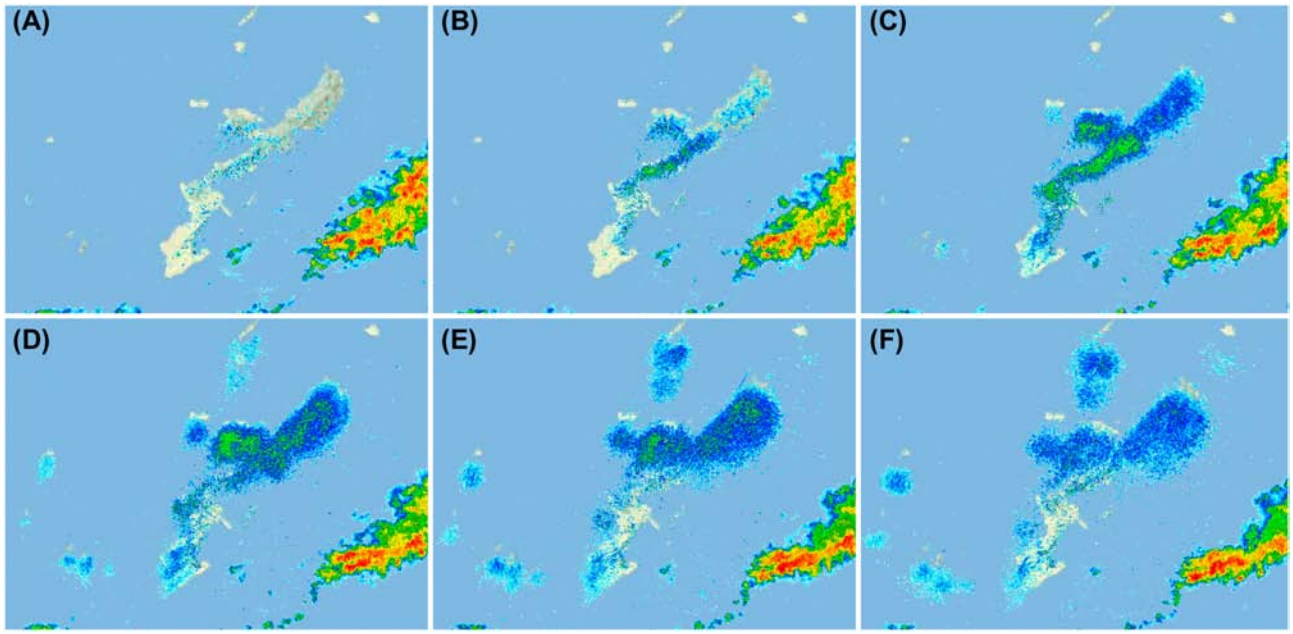

Figure 4. The dusk ascent of migrating birds from stopover sites on the Okinawa Islands on 23 September 2017 as observed by the Kadena radar at (A) 09:36 UTC, (B) 09:42 UTC, (C) 09:48 UTC, (D) 09:54 UTC, (E) 09:59 UTC, and (F) 10:05 UTC. Sunset occurred at approximately 9:24 UTC. Persistent signals to the east of the islands are rainstorms.

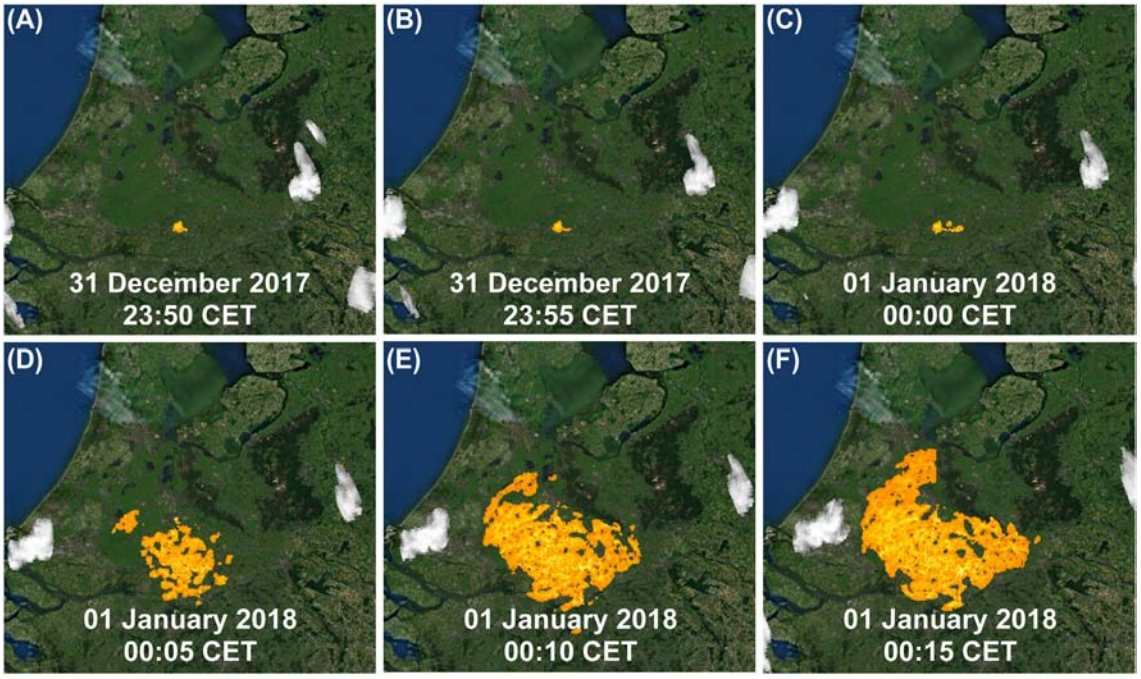

Figure 5. The midnight ascent of roosting birds over the Netherlands on New Year's Eve, disturbed into flight by widespread fireworks as seen by weather radar. Radar reflectivity factor contributions are identified as weather (greyscale) or birds (orange) based on dual-polarization information.

years using WSR. Thousands of birds took flight shortly after midnight, with high aerial movements lasting at least 45 min and peak densities measured at 500 m altitude. The authors estimate that hundreds of thousands of birds in the Netherlands take flight due to fireworks. Highest densities were measured over grass- and wetlands where thousands of waterfowl rest and feed (including nature conservation sites and resting areas of international importance).

Fireworks and other methods such as water cannons are also used, sometimes illegally, to disperse roosts or breeding colonies of bird species that establish in locations where they can become a nuisance, and (near) real-time radar monitoring may provide an alert of such activities. When persistent roosting sites are known for birds (Bridge et al. 2016) or bats (Horn and Kunz 2008, Stepanian and Wainwright 2018), flights from these sites can be monitored by radar to establish baselines of population size, distribution and persistence. Subsequent measurements that deviate from these patterns, such as a sudden change in roost location or size, can be indicative of adverse disturbances or varying environmental conditions, although day-to-day roost locations for some species can be quite variable.

Nocturnally active animals move through skies which are increasingly light polluted in radiance and extent. Earth's artificially lit outdoor area grew by 2.2% yr^{-1} from 2012 to 2016, with a total radiance growth of 1.8% yr^{-1}. Continuously lit areas have brightened at a rate of 2.2% yr^{-1} (Kyba et al. 2017). Artificial light can impair orientation and navigation and may attract insects and migrating birds in large numbers as well as foraging and migrating bats. This artificial mixing of predators and prey can also influence foraging behaviour and even result in competitive interactions among predators (Shields and Bildstein 1979). Aerial animals may collide with artificially lit structures such as lighthouses, lightvessels, communication towers, wind turbines or other large buildings, but also with offshore oil and gas-rigs, platforms and even brightly lit ships (Eisenbeis 2006, Gauthreaux and Belser 2006, Drewitt and Langston 2008, Ballasus et al. 2009, Mathews et al. 2015, Hüppop and Hill 2016, Hüppop et al. 2016). Birds might also get 'trapped' by artificial light (Verheijen 1960, Gauthreaux and Belser 2006) and eventually die due to exhaustion (Hüppop et al. 2016). That birds and other animals respond to artificial light has been known for more than a hundred years, but these behaviours are still poorly understood (Gauthreaux and Belser 2006). Using a 'true' tracking radar (i.e. a radar with an antenna which follows a selected target automatically, Table 1), Larkin and Frase (1988) found that birds circled (at least partly) a 308 m broadcasting tower equipped with red slow-blinking and steady lamps, at distances of 108 to 279 m in cloudy conditions (a concentration of birds near the tower was not noted). Under clear skies or beneath cloud layers, these circles were not observed, and it could not be determined if individual birds circled the tower repeatedly (Larkin and Frase 1988). Switching a strong searchlight on and off parallel to the radar beam while tracking single nocturnal migrants by radar also induced pronounced reactions, including a wide variation of directional shifts, a mean reduction in flight speed to 15–30% of normal air speed

and a slight increase in climbing rate after the light was switched on (Bruderer et al. 1999).

WSRs allow assessment of the effects of artificial lights on nocturnally migrating birds on a much broader scale than small mobile radars, which provide information on more local impacts. Using multi-year WSR measurements of nocturnal migrants across the northeastern U.S., McLaren et al. (2018) showed that autumnal migrant stopover density increased at regional scales with proximity to the brightest areas but decreased within a few kilometers of brightly-lit sources, which implies broad-scale attraction to artificial light while migrating. Van Doren et al. (2017) studied effects of the beams of the National September 11 Memorial and Museum's 'Tribute in Light' in New York on nocturnal migrants with radar and acoustic sensors. This single high-intensity light source induced significant behavioral alterations up to altitudes of 4 km, even in conditions with good visibility. When the installation was illuminated, birds aggregated in high densities (20 times greater than surrounding baseline densities), decreased flight speeds, changed radial velocities, and vocalized frequently. Simulations revealed a high probability of disorientation and subsequent attraction of nearby birds, indicating the beams influenced the behaviour of birds in airspaces considerably beyond those immediately occupied by the display. The behavioural disruptions disappeared when lights were switched off.

For assessing the collision risk of birds with man-made structures and implementing mitigation measures, it is essential to know how many birds fly at 'risky' altitudes (Bruderer and Liechti 2004). Marine radars set up to rotate on a vertical plane have been used in a multitude of studies to investigate the altitudinal distribution of birds, especially of nocturnal migrants, close to transmission lines, wind turbines, communication towers and other man-made structures (examples in Gauthreaux and Belser 2003, Desholm et al. 2006, Hüppop et al. 2006, Fijn et al. 2015 and Bruderer et al. 2018). However, identification of taxonomic groups is only feasible in very few cases, requiring the use of other methods to supplement the radar data. Therefore, distance-dependent quantification is technically difficult or impossible, and height profiles have to be taken with caution (Schmaljohann et al. 2008, Beason et al. 2013). Nevertheless, these studies are in accordance with others made with calibrated pencil-beam radars, showing the most intense migration at low levels and a pronounced decrease with increased height: 20 to 30% of nocturnal onshore bird migration in Europe and North Africa takes place in the lowest 200 m interval, 50% below 700 m a.g.l., and the 90% quantile reaching heights between 1400 and 2100 m a.g.l. The remaining 10% of migrants are usually scattered up to about 4000 m a.s.l. (Bruderer et al. 2018). As determined by modified marine or special purpose bird tracking radar, more than one third of the migrants in the offshore North Sea were flying in the lowest 200 m a.s.l., i.e. in or below the rotor swept area of wind turbines (Hüppop et al. 2006, Fijn et al. 2015). Although altitude distributions can also be derived from WSR data (Dokter et al. 2011), they only cover the lower altitudes – where birds and bats might collide with anthropogenic structures – very near the radar. The distance from WSRs at which their altitude profiles still apply remains an open question in relation to monitoring airspace use by birds and bats flying in the vicinity of tall man-made structures.

In general, radar studies are particularly useful in estimating numbers of birds and bats and their behaviour near wind farm infrastructure (Johnson et al. 2002, Desholm et al. 2006, Kunz et al. 2007, Ahlén et al. 2009, Villegas-Patraca et al. 2014, Hein 2017, Smallwood 2017, Hüppop et al. 2019, Molis et al. in press). Bird detection radar was used to monitor behavioural responses and flight changes of migrating common eider *Somateria mollissima* and geese in relation to offshore wind farms and helped to evaluate wind farm avoidance rates (Desholm and Kahlert 2005, Plonczkier and Simms 2012). Radar-based methods also have been successfully used to quantify great white pelican *Pelecanous onocrotalus* flights in the vicinity of a planned wind farm on the coast of South Africa and model the turbine collision risk (Jenkins et al. 2018). Sandhill cranes *Grus canadensis* were likewise monitored in flight in the vicinity of wind turbines and exhibited avoidance except in the presence of fog when flight behaviour became significantly more circular, possibly increasing the likelihood of turbine collision (Kirsch et al. 2015). Fijn et al. (2012) studied the behaviour of Bewick's swans *Cygnus columbianus bewickii* wintering near a wind farm in the Netherlands. The swans adjusted their flight-paths to the presence of the wind turbines during both light and darkness by flying around individual turbines and between rows of turbines. Aschwanden et al. (2018) combined data from a dedicated bird radar on movement intensities with collision data from carcass searches near to wind turbines. Collisions mainly occurred during migration, but not necessarily in mass migration events, and primarily affected nocturnal migrating passerines. Stumpf et al. (2011) used a marine radar to measure flight altitudes of marbled murrelets *Brachyramphus marmoratus* transiting to and from breeding sites to improve predictions of collision risk with future coastal wind farm developments. 4.6% of murrelets were flying at or below the average wind turbine rotor-swept height of 130.5 m. According to recent findings, radar-based approaches are suggested for continuous monitoring of bird interactions with offshore oil and gas platforms (Ronconi et al. 2015) and for long-term impact assessments at offshore wind farms (Hüppop et al. 2002, Desholm et al. 2006, Plonczkier and Simms 2012).

At greater spatial scales, WSR products could be used to measure the temporal and spatial components of avian migration and provide near real-time assessment of threats of mortality from anthropogenic structures, such as wind turbines and buildings (Shipley et al. 2017). For example, WSR (and other radars) can be used to identify periods with high flight activity of birds and bats where wind turbines should be slowed or shut down to reduce mortality by collision or

barotrauma (Arnett et al. 2011, 2016, Marques et al. 2014, Tomé et al. 2017).

While human safety has been of paramount concern to civil aviation regulatory agencies and the military, the proliferation of unmanned aerial vehicles (UAVs) also poses novel challenges to future airspace management and conservation. Depending on the type of UAV, they also likely affect the ecology and behaviour of flying animals and might cause resting birds to take off if they are disturbed (Lambertucci et al. 2015, McEvoy et al. 2016). As with the studies on birds' reactions to fixed obstacles, radar could help to further investigate how birds and bats respond to UAVs. However, this requires that these targets can be identified by radar. Molchanov et al. (2014) developed a chain for automatic target recognition of UAVs based on micro-Doppler signatures (Doppler modulations of the returned signal caused by micro-motion dynamics of the target; Gürbüz et al. 2015) that can be used with continuous wave radar or radars with high pulse repetition frequencies.

Marine radar was also used to investigate disturbance effects of ship traffic on waterbirds. In the North Sea and Baltic Sea, Bellebaum et al. (2006) measured flight distances of divers *Gavia* spp., long-tailed duck *Clangula hyemalis* and velvet scoter *Melanitta fusca* by the research vessels' onboard radar. Perpendicular flight distances from the course of the vessel were 400 m (median) and 1000 m (90% percentile), respectively, for divers, 400 m and 700 m for velvet scoter and less than 200 m and 600 m for long-tailed duck. Kaiser et al. (2006) observed that common scoters *Melanitta nigra* were in low abundance or absent from areas in which shipping activity was relatively intense, even when these areas held a high prey biomass. Flight distance as measured by radar varied according to flock size. Larger flocks flushed at distances from 1000 to 2000 m, while small ones flushed at distances of less than 1000 m.

Radar might also be useful to deter birds and bats from sites bearing risks for them. Ronconi and St Clair (2006) developed a radar-activated on-demand system for deterring waterfowl from oil sands tailings ponds. Nicholls and Racey (2009) found that pulsed electromagnetic radiation from a small mobile radar can reduce bat activity close to the radar's fixed antenna. Although the mechanism through which behaviour could be affected in this manner is unclear, the authors suggest that electromagnetic radiation even from small radars might discourage bats from approaching wind turbines and thus reduce collision risk. However, this is yet to be tested at an operational wind farm (Arnett 2017).

Foraging and habitat use

Studies of migration have comprised the main use of radar in entomology and ornithology, but radar techniques have also been applied to studies of non-migratory 'station keeping' behaviours, such as foraging (in the wide sense of appetitive movements to find the resources required for survival, somatic growth and reproduction; Dingle 2014). The application of radar to insect foraging is reviewed in Drake and Reynolds (2012, chapter 14). The main technology employed in these studies has been harmonic radar (Drake and Reynolds 2012, chapter 8; Kissling et al. 2014), where a transponder is attached to the individual to be tracked. This device returns signals to the radar at twice the transmitted frequency and, because the receiver is selectively tuned to this shifted frequency, all unwanted radar reflections ('clutter') from ground features (which would normally obscure a low-flying insect target) are suppressed. There are two forms of entomological unit using the harmonic principle: azimuthally-scanning 'true' radars which provide geometrically accurate maps of the insects' flight trajectories, and harmonic direction-finders – portable instruments which do not provide range information but allow the operator to move in the direction from which the strongest signals are received, and thus home in on a tagged insect much as one might using traditional radio tracking.

Azimuthally-scanning harmonic radar is particularly suited to bee tracking studies, and this technology has already furthered work on bee navigation and pollinator ecology (see references in Drake and Reynolds 2012, Lihoreau et al. 2012 and Woodgate et al. 2016), as well as documenting the (deleterious) effects of sub-lethal doses of neonicotinoid insecticides and glyphosate herbicide on bee foraging behaviour and navigational performance (Fischer et al. 2014, Balbuena et al. 2015, Tison et al. 2016). These studies form part of the accumulating evidence of harm to wild bees and honeybees by neonicotinoids in the environment and will have assisted in informing the probable ban on all uses of these insecticides on outdoor crops. There have also been scanning harmonic radar studies of foraging and short-range dispersal in butterflies (Cant et al. 2005, Ovaskainen et al. 2008), indicating that this technique can be applied to taxa other than bees (see also Kissling et al. 2014).

Harmonic direction-finders have been used mainly on studies of pest insects, but also on some beneficial species such as natural enemies of pests (e.g. carabid beetles) and on other (non-insect) invertebrate species of conservation concern (see references in chapter 14 of Drake and Reynolds 2012, Kissling et al. 2014). The study species often disperse by terrestrial locomotion or, if they can fly, do so mainly over short distances only. Useful information on the localized flight of more mobile species (e.g. dragonflies; Hardersen 2007) has also been obtained by this technology. Allied techniques such as radio telemetry have also been employed on insects large enough to carry active transmitters (reviewed by Kissling et al. 2014). A typical example might be the monitoring of short-range dispersal flights of an endangered scarabaeid beetle *Osmoderma eremita* which lives in old hollow trees (Hedin et al. 2008, Svensson et al. 2011).

In contrast to entomology, radar has rarely been applied to study foraging or other local movements of individual birds and mammals. Active radar transponders were used to trace coyotes *Canis latrans* and further developed to be used e.g. in seabirds (French and Priede 1992). At least under calm

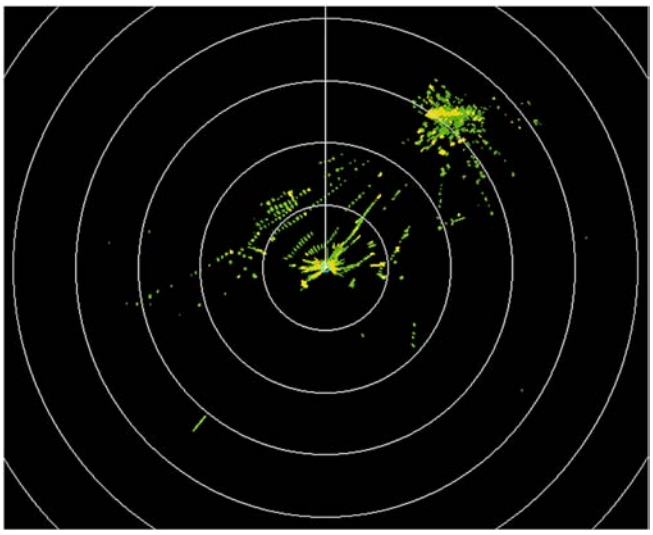

Figure 6. Tracks of gulls approaching and foraging at a fishing vessel (upper right corner) as visualized by an off-the-shelf X-band marine radar (25 kW peak power) installed on a research platform in the southern North Sea (distance between rings: 1 nautical mile). Herring gulls *Larus argentatus*, great black-backed gulls *Larus marinus* and other gulls use the helicopter deck of the platform for resting and to 'wait' for fisheries activities to feed on discards and offal (Hüppop et al. 2008).

weather conditions, birds interacting with fishing vessels (Fig. 6, Assali et al. 2017) or bats foraging over the open sea (Ahlén et al. 2009) can be observed by marine radar. Many seabird species feed in large numbers at fishing vessels on offal or bait, where their high mortality is the main threat to populations worldwide (Phillips et al. 2016). But the extent of overlap and behaviour in relation to ships is poorly known (Fig. 6). Using novel biologging devices, which detect radar emissions and record the position of boats and seabirds, Weimerskirch et al. (2018) measured the extent of the overlap between albatrosses and fishing vessels and generated estimates of the intensity of fishing and distribution of vessels in international waters, which has widespread implications for bycatch risk in seabirds and identification of areas of intense fishing throughout the ocean.

Analysis of WSR data has revealed that densities of waterbirds increased in response to temporary wetland habitat established for migrating birds, following the Deepwater Horizon oil spill in the Gulf of Mexico (Sieges et al. 2014). Similarly, densities of waterfowl as measured by WSR increased in response to restoration of wetland habitat as part of the Wetland Reserve Program in the U.S. (Buler et al. 2010). In both of these examples, access to archived WSR data proved critical to establishing baseline measures of bird use prior to habitat alteration.

Perspectives and challenges

While radar has been used to study animal movements for almost three quarters of a century, the recent advancements in radar technologies and data processing, namely the establishment of networks of WSRs across the globe and the development of software to extract biological targets from the radar products (Dokter et al. 2019), offer a tremendous opportunity for comprehensively tracking and monitoring the movements of large numbers of flying animals across vast spatial scales (Fig. 1).

Furthermore, the combination with other techniques, such as dedicated special purpose radars, trapping and ringing, biologging, citizen science data like eBird in the U.S. (<https://ebird.org>) and Ornitho in Europe (e.g. <www.ornitho.de>), visual and acoustic bird counts, or thermal imaging can provide further information on the identity of the animals observed in the airspace, which still remains a major challenge in radar aeroecology (Desholm et al. 2006, Jarrah et al. 2013, Drake and Bruderer 2017, Molis et al. in press). Classification and quantification of aerial targets and their biomass will become more feasible with continuing technical advances, for example in hardware upgrades such as radar polarimetry, knowledge of species specific radar cross sections under various aspects, wing beat frequencies, flight speeds and characteristics of meteorological targets (Vaughn 1985, Zaugg et al. 2008, Dokter et al. 2011, Nohara et al. 2011, Stepanian et al. 2014, Gürbüz et al. 2015, Drake 2016, Mirkovic et al. 2016, 2018, Chilson et al. 2017, Drake et al. 2017, McCann and Bell 2017).

In the near future, existing or developing networks of other types of radar might become of broader use in aeroecology and biological conservation, too, e.g. those of windprofilers (which are designed to detect turbulence in the atmosphere; Gürbüz et al. 2015, Weisshaupt et al. 2017, 2018) or air traffic surveillance.

Taking advantage of large-scale radar networks in the longer term will elucidate the effects of global change in time and space of flyways, stopover and wintering site use, roosts (change in size, phenology and location), populations and numbers (including estimates of gross reproductive success and mortality; Dokter et al. 2018) of aerial animals. Standardized monitoring programs will act as an early large-scale warning system for population declines and may be used to complement data from other sources. For example, recently documented declines in insect biomass in Europe (Biesmeijer et al. 2006, Hallmann et al. 2017) may serve as an early indication of larger-scale issues concerning ecosystem health given the critical role that insects play in the majority of terrestrial habitats, for example as herbivores, pollinators, and as food for other animals.

Operational radar monitoring of pest insects, by facilitating earlier interventions, more efficient, targeted control, and thus considerably reduced pesticide application, will not only have economic but also indirect positive effects for conservation. The indiscriminate application of pesticides has been shown to have far-reaching ecosystem consequences and have been associated with population declines of farmland birds (Mineau and Whiteside 2013, Hallmann et al. 2014, Stanton et al. 2018), and beneficial insects such as pollinators (Gilburn et al. 2015, Goulson et al.

2015). Routine observations from operational and research WSR have already been incorporated into a warning system for aphids and other migratory insect pests invading southern Finland; early detection of the pests provided extra time in which to implement control measures (Leskinen et al. 2011). Vertical-beam entomological radars are a useful component of the decision-support system for management of Australian plague locusts *Chortoicetes terminifera*, by serving as 'sentinels' alerting forecasters of significant nocturnal movements (Drake and Wang 2013). Similar early warning systems could be applied far more widely to target pest management activities by monitoring pest species movements before numbers reach critical levels or by identifying source populations.

Application of knowledge of migratory bird natural history and the response of flying animals to weather conditions (Becciu et al. 2019) will further assist in the development of radar based predictive models to forecast migration and other movements (Shamoun-Baranes et al. 2008, Van Doren and Horton 2018, Nilsson et al. 2019) which can be relevant for conservation. Doppler-WSR offers the unique opportunity to measure weather (wind and rain as important variables influencing e.g. bird and insect migration intensity) and aerial animal movements simultaneously with the same sensor (Trombe et al. 2014).

For the Netherlands and Belgium, the FlySafe Bird Avoidance Model provides near real-time information and forecast on large scale bird mobility in the air space, including bird density measurements, predictions and altitude profiles (Ginati et al. 2010, <www.flysafe-birdtam.eu>). The German Army Geoinformation Office issues notices on passage of flocks of birds through airspace (BIRDTAM; <www.notams.faa.gov/birdtam>). Recently, Van Doren and Horton (2018) developed models for forecasting bird migration across the United States. Such predictions could contribute to the conservation of migrants by providing an early warning system, for example by allowing stakeholders to switch off wind turbines or artificial lights at critical moments, thus reducing mortality while keeping economic losses low. Near real-time analysis of WSR data can be used for creating bird-avoidance models to forecast risks for collisions between birds and aircraft (Shamoun-Baranes et al. 2008, van Gasteren et al. 2019, <www.flysafe-birdtam.eu>, <www.notams.faa.gov/birdtam>).

Radar will play an increasing role in revealing the ecology of the airspace and in conservation planning and monitoring of flying animals and their habitats. Radar data have become a standard source of information on ecosystem structure, composition (despite its limitations in identifying taxonomic groups), and function in ways that will inform on the wider spatial and temporal changes occurring globally. Radar can be used to identify where flying animals concentrate into hot-spots that may be occupied seasonally or throughout much of the year. The proliferation of aerial man-made structures – from communications towers through wind turbines to UAVs – increases the likelihood that environmental law will eventually encounter the concept of aerial habitat. This is already happening in New Zealand (Wallace 2007) and anticipates a time when aerial conservation reserves become reality as part of larger species preservation networks that include all forms of habitat.

Given the trajectory of recent research, it is apparent that radar will continue to advance our knowledge of the biology of birds, bats, insects, and other aerial biota. The larger challenges lie in developing the technical, legal, and educational infrastructure required to actually put these advances into practice toward the conservation of flying animals.

Acknowledgements – Felix Liechti and Hans van Gasteren provided key input for Table 1.
Funding – We gratefully acknowledge the support provided by the COST – European Cooperation in Science and Technology Action no. ES1305 'European Network for the Radar Surveillance of Animal Movement' (ENRAM). MHMM was partly supported by COST STSM ES1305-38062 and the Burgergemeinde Bern. Rothamsted Research receives grant-aided support from the United Kingdom Biotechnology and Biological Sciences Research Council (BBSRC).

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