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Mapping migratory routes: Avian conservation-focused opportunities for a pan-European automated telemetry network

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Accelerated biodiversity loss during the Anthropocene has destabilised functional links within and between ecosystems. Migratory species that cross different ecosystems on their repeated journeys between breeding and non-breeding sites are particularly sensitive to global change because they are exposed to various, often ecosystem-specific threats. As these bring both lethal and non-lethal population impacts, many migratory species are declining, making this group especially vulnerable to global change.

To mitigate their decline, research at a continental and flyway scale is required to adequately monitor changes in the migratory and demographic processes of populations during all parts of the annual cycle. The Motus Wildlife Tracking System (Motus) could provide a solution to data gaps that exist particularly for small, migratory species. Motus is an automated telemetry system for animal tracking, which provides a collaborative network by using a single VHF radio frequency for all tracked individuals, in combination with an individual tag identifier. Motus can provide information on movements made by individuals of small migrant species, thus aiding our understanding of aspects of their migration that could impact demographic parameters.

Here we describe conservation-focused research opportunities, with a particular lense on small European migrant birds. We highlight examples from the existing network, and identify geographical gaps which, if filled, could track continent-wide movements. We conclude that Motus is a useful tool to produce individual-level migration information for a variety of small-bodied taxa, and that a drive to expand the network will improve its ability to direct conservation plans for such species.

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Introduction

Biodiversity loss driven by land use change, exploitation of natural resources, and affected further by climatic disruption, is a defining feature of the Anthropocene (Sala et al. 2000). A decline in habitat availability and disruption to ecosystem structure, reducing critical services such as nutrient cycling, carbon storage and flood control, has led to declines in a wide range of taxa globally (Jaureguiberry et al. 2022). The impacts of anthropogenic development do not just manifest through physical changes, i.e. habitat loss, but also through increases in zoonotic and vector-borne diseases (Jaureguiberry et al. 2022), and pest outbreaks (Ayres and Lombardero 2018). These impacts affect species' distributions, abundances, fitness, and consequently their ability to complete their life cycle successfully (Bellard et al. 2012).

Of particular concern are migratory species, which serve as ecological indicators and providers of vital contributions to ecosystem functioning, including biomass production, pollination, and pest control (Bauer and Hoye 2014, Satterfield et al. 2020). Migratory species experience a variety of environmental conditions on their seasonal, sometimes inter-continental journeys (Turbek et al. 2018, Zurell et al. 2018; Horton et al. 2020; Howard et al. 2020). Rapid changes in land use and configuration, throughout their annual cycle, can mean that their requirements for reproduction and survival are compromised (Birnie-Gauvin et al. 2020, Marcacci et al. 2022, Rigal et al. 2023). There are also additional threats such as (illegal) hunting (Jiguet et al. 2019), the extension and complication of ecological barriers (Gauld et al. 2022), as well as increasingly unpredictable climatic patterns decoupling the phenology of ecologically linked species (Iler et al. 2021, Clarke et al. 2022).

These challenges directly conflict with the multi-factorial optimisation of migration, which is often based on inherited, integrated migration strategies (Åkesson and Helm 2020; Schmaljohann et al. 2022, Fattorini et al. 2023). While migrant species differ in their migratory timing, distance, speed, and route, their journeys all involve repeated, alternating migratory endurance flights and stopover periods for resting, recovering and fuelling (Alerstam et al. 2003; Åkesson and Hedenström 2007; Schmaljohann et al. 2022). Understanding the factors impacting population trends of these species, i.e., the changes in vital rates that drive population growth or decline, is essential (Morrison et al. 2016), as many migratory species cannot respond to changes at a sufficiently rapid pace, producing widespread population declines (Both et al. 2006, Wilcover & Wikelski 2008, Frick et al. 2020, Rosenberg et al. 2019, Vickery et al. 2023).

The Convention on the Conservation of Migratory Species highlights the need for a multi-species, flyway level perspective in terms of research into population declines (UNEP/CMS 2020, Frick et al. 2020, Marcacci et al. 2022, Chowdury et al. 2023, Vickery et al. 2023). However, gathering data from a sufficiently high number of individuals from different populations at this scale, is extremely challenging (Morrison et al. 2016; McKinnon and Love 2018), and reliant on international collaboration (Nadal et al. 2020; Vickery et al. 2023, Serratosa et al. 2024). Particularly for small and light migratory passerines, waders and highly aerial species such as swifts, their size and behaviour have rendered it difficult to study their movements (Wikelski et al. 2007, Fiedler 2009).

Current methods and their limitations

Studying when and where differences in population processes occur in migratory birds is notoriously difficult (Doerr and Doerr 2005; Border et al. 2017, Telensky et al. 2020). However, quantifying variation in survival, mortality, emigration and immigration (summarized as dispersal), is crucially important to formulate effective conservation measures for populations and species that are at risk of decline (Gómez et al. 2021, DeMars et al. 2023).

Currently, we have little detailed spatial and temporal information on migrating small birds. Broad scale migration patterns across Europe, including concentrations of both avian and insect migrants passing through marine and mountainous regions, have been identified using radar (Bruderer & Jenni 1990, Bruderer & Liechti 1999, Nilsson et al. 2019, Weisshaupt et al. 2021, Hirschhofer et al. 2024). Yet radar data largely do not allow us to tease out species-specific and individual-level variation in large-scale movements (Schmaljohann et al. 2008, Zaugg et al. 2008), which would facilitate links to demography, physiology and ecology.

In contrast, several million individuals have been marked using metal or colour rings across Europe (Du Feu et al. 2016, Spina et al. 2022), contributing to our fundamental knowledge of bird movements. Yet recapture, recovery, and resighting probabilities are largely low (across 32 European level ringing schemes, recovery rate for *all species combined* varied from 0.6 – 7.6%; Baillie 1995). This is particularly the case on the wintering grounds but is highly variable amongst species and locations (Thorup et al. 2014). For example, the Willow Warbler (*Phylloscopus trochilis*) is ringed in huge numbers on its breeding ground in northern Europe, but only a very small number of recoveries take place in Africa. Specifically, in Finland, about 16000 individuals of this species need to be marked on the breeding grounds for each recovery in sub-Saharan Africa (Hedenström and Pettersson 1987).

We can address the disadvantages of these methods by tracking individual migratory, pre- and post-breeding dispersal (Mukhin et al. 2005, Züst et al. 2023), and nomadic, non-breeding movements (Snell et al. 2018; Mckinnon et al. 2019). However, individual tracking of small migrants requires tracking devices weighing a maximum 3-5 % of an individual's body weight (Barron et al. 2010), which excludes most tracking technology on the market (Figure 1; Bridge et al. 2011, McKinnon & Love 2018), including new low-power, wide area devices such as SigFox or LoRaWAN (Wild et al. 2023). Radio- transmitters, however, have already reached minimum weights of currently 0.13 g (Lotek NanoPin), lighter than the smallest light-level geolocators (Lotek: 0.3 g), and significantly smaller than GPS units which require significant energy to relay information to a satellite and fix a position. Some radio-tracking systems, e.g., the tRackIT System and the ATLAS project, have narrow spatial coverage and a limit on how many individuals (c. 200) they can monitor concurrently (Gottwald et al. 2019, Beardsworth et al. 2022).

The Motus Wildlife Tracking System (Motus) exploits a network of VHF receiving stations aligned on the same frequency, which continuously receive and record uniquely coded signals of tagged individuals using mostly directional Yagi antennae without the need for recapture (Taylor et al. 2017, Imlay et al. 2020). Here, we focus on filling conservation and demographic-specific knowledge gaps using Motus to track migratory birds, and we hope to further spark the collaborative spirit of Motus to create a denser network in Europe and resemble the situation in North America.

Motus and its benefits

Motus originated in Canada as a partnership between Acadia University and Birds Canada (Taylor et al. 2011, 2017), and its spread across the Americas is a great success story of collaborative research (see https://motus.org). Globally, to date (December 2024) there are now 875 established tagging projects, which combined have tagged 50,688, animals of 402 species. The entire Motus network at the moment consists of 2060 receivers, and the largest single project array consists of 109 receivers in Ontario.

Publications resulting from Motus data total 214, which combined were cited according to Zotero >500 times. The number of publications based on Motus data has more than doubled since 2015/16 (Figure 2), and the lead and coauthors of these publications are rarely just limited to academics; the application of Motus has been recognised by multiple stakeholders such as the US Fish & Wildlife Service (USFWS), National Parks Service (NPS), Canadian Wildlife Service (CWS) and BirdLife Europe (Machado et al. 2024).

Investment in the network across North America continues to grow, including in March 2024 a grant of $3.1 million CSD awarded to a consortium of five Canadian universities and Birds Canada to continue installing Motus receiving stations across the country, as well as to invest in community-based science. This investment, combined with a specific mention within the CMS of automated radio tracking deployed at a flyway scale (COP13, Resolution 12.26) demonstrates the value, and potential future value, of Motus to conservation.

The initiation of Motus in Europe started in 2017, and although the network has grown slower than in the Americas there is now a dense network of passive receiving stations (e.g. Figure 3) along the coasts of Germany, the Netherlands, and the UK, and to a slightly lesser extent in Sweden, Denmark, Belgium and France, with a number of additional stations in other countries, and offshore (Figure 4).

The network of stations in Europe is still patchy, particularly in eastern Europe, and there is a lack of a universally-permitted tracking frequency, so does not yet allow continuous tracking across the continent. In many European countries, the frequency of 150.1 MHz is authorised either temporarily or permanently for wild animal telemetry tracking. Multi-frequency detection by Motus receivers is possible, but it incurs additional expense for extra equipment. For example, adding antennas to receiving stations for monitoring the license-free frequency of 434 MHz would cost approximately €80 – 300 per station, for an additional 1 - 4 antennas, plus the extra cost of cables. For the tags, researchers can select from among a number of options and device parameters, including burst interval (usually from 1 s to 1 min), battery or solar power, attachment and antenna type, in line with their specific scientific requirements (Figure 1).

Motus has many promising features, including its extended temporal and spatial data gathering capacity, compared to standard radio-tracking. In addition to autonomous, near-real-time recording of the receivers and sub-0.5 g tags, the spatial scale of detections is in the order of several kilometres, rather than orders of magnitude higher as with geolocators (Taylor *et al.* 2017), although new multi-sensor tags have shown substantial improvements in positional accuracy (Nussbaumer et al. 2023). Receiving stations can, in theory, be placed anywhere (see Figure 3b) and have a 10 kilometre-plus detection range, and therefore data capture is less limited by researcher effort, in contrast to commonly used methods such as bird ringing (Griffin et al. 2020; Flack et al. 2022). Fixed positioning of the receiving stations (ideally at sites of importance to the species of interest to maximise detection probability), along with an unrestricted recording period, also enables standardized data collection, reducing observer-bias (Griffin et al. 2020).

Despite the advantages, there are drawbacks of radio-tracking studies in general. Most studies do not detect all of the individuals which are tagged; the reasons for this are many and are not mutually exclusive, but can include loss of the tag, predation, emigration, tag failure, topography or weather conditions. Crewe et al. (2020) reported rates closer to 50-70%, whereas a dense coverage of receivers on the small island of Helgoland repeatedly resulted in detection rates of 95-100% (Karwinkel et al. 2022, 2024). There are also uncommon occurrences of high levels of ‘false positive’, or uncoded detections, which can appear if large numbers of individuals are released at once close to a receiver. Mitigations, such as staggered switching on of the tags to encourage differential pulse emission, can be put in place, and the numbers required to cause this confusion mean this is unlikely to happen in a ‘natural’ scenario.

Motus is already producing important insights into the movements of migrating and wintering European birds, including a better understanding of the migratory and pre-migratory movements of sea-crossing thrushes (Brust et al. 2019) and differences between long and short distance migrants in stopover time and flight direction (Packmor et al. 2020, Rüppel et al. 2023). Examples from Europe and North America show that Motus can gather long-term, annual cycle data, in a relatively low-cost manner, on groups and time periods (e.g. juvenile fledging) that are often missing from population studies (Satterfield et al. 2020, Martell et al. 2023).

How Motus can help to address knowledge gaps in small migratory bird movement by collecting demographic information.

Survival and mortality

Despite the biological significance of survival and mortality on population size and its dynamics (Sandercock 2020), little is known about both rates in migratory passerines. Within migratory species, variation in survival among populations can be linked to alternative routes and their different pressures (Hewson *et al.* 2016). The latter may increase population-specific immediate and delayed fitness costs (Dhanjal-Adams et al. 2017), which might be particularly prevailing in those areas that support high numbers of ‘co-migrants’ (multiple species moving through major sites and corridors simultaneously – Cohen et al. 2020). The convergence of otherwise spatially segregated populations at single locations may also increase the probability of disease transmission with delayed fitness costs (Cohen et al. 2020).

To obtain information on route- or area-specific mortality rates, focusing receiving station placement in closely packed ‘fence’ or ‘curtain’ formation (Figure 4) would provide ‘checkpoints’ for tagged migrants along their migratory routes. If there are sufficient stations intersecting migratory routes (and adequate numbers of individuals are tagged), then obstacles that slow down migration can be identified, alongside estimates of mortality rates for such areas (Klaassen et al. 2014, Buechley et al. 2021). Survival has been successfully estimated using Motus for the Kirtland’s warbler (*Setophaga kirtlandii*; Cooper et al. 2024). This species’ limited population size and discrete wintering range, lends itself to Motus, and a robust design Cormack-Jolly-Seber model allowed the calculation of apparent survival rates with a high level of certainty, knowing that a high proportion of marked individuals had been detected.

Gonzalez et al. (2021) used Motus to identify habitat-specific overwinter survival rates in the Swainson's Thrush (*Catharus ustulatus*), which can be used to inform habitat protection and management on the wintering grounds. Motus has also been used by Brunner et al. (2022) to identify high migratory connectivity amongst populations of the elusive Swainson's warbler (*Limnothlypis swainsonii*), which has implications for population-specific changes and can direct future monitoring work. These cross-continental studies demonstrate the power of Motus to collect data at multiple scales, helped by the fact that tags do not need to be recaptured to retrieve the data, therefore reducing bias. Extensive testing of detection capability of an antenna array in a fixed area, is essential to maximise coverage and the ability to produce survival estimates. Better still if survival is estimated across a limited area (Cooper et al. 2024) and restricted temporal period to increase the robustness of the estimates (Evans et al. 2020, Bliss et al. 2020).

Identification of Stopover sites

Motus can be used in regional arrays that expand outwards from a known stopover site, allowing identification of exploratory and regional movements by birds that may be assessing the wider area, often undertaken at night (Taylor et al. 2011, Brown and Taylor 2015, Schmaljohann & Eikenaar 2017). In Europe, this could build on current ringing efforts at hotspots (e.g. Bay of Biscay; Strait of Gibraltar) but at spatial scales not feasible for ringing. Pinpointing specific sites for targeted conservation efforts is important, where limited, localised stopover site use could induce higher vulnerability in certain migrating species (Bayly et al. 2013, Gómez et al. 2014, Hagelin et al. 2021).

Temporal information on arrival and departure time, using Motus on multiple individuals of different species, can help with elucidating the functions of stopover sites (Moore 2018, Linscott and Senner 2021, Schmaljohann et al. 2022). Identification of these functions could be very valuable in the context of future global climate change, when the current conditions of stopover sites may degrade, or they might even disappear completely (Bayly et al. 2018). Smetzer and King (2018) used a regional Motus network to identify a major stopover area for Blackpoll warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceous*) in the Gulf of Maine of the United States. The prolonged stopovers recorded by both species suggest that the region may serve as a major refuelling area when preparing for long-distance migratory endurance flights, thus demonstrating the area's high conservation value.

Stopover sites on either side of ecological barriers, could be equipped with Motus stations in high densities, (e.g. distance of 5 - 10 km between stations but variation in detection distance due to topography and the behaviour of the species must be taken into account), to provide insights into how birds respond to such barriers (e.g. Sjöberg et al. 2015, Zenzal et al. 2021). This might include local to regional scale movements before crossing, intrinsic and extrinsic conditions required for a successful crossing, stopover duration, departure directions, and potential differences between populations and seasons. Both Holberton et al. (2019) and Herbert et al. (2022) used Motus to demonstrate site-based variation in stopover duration, which was related, at least in part, to bird condition and morphology. This indicates some level of migratory connectivity, and as such, loss, or degradation of one or more stopover sites could have population level implications.

Dispersal, immigration and emigration

Natal and breeding dispersal are critical but understudied fundamental biological processes, partly because nestling and juvenile survival is generally so low that high manpower and financial investment is required to track a few individuals. Dispersal consists of the initial process of emigration from a breeding site, and the subsequent immigration to another (Matthysen & Clobert 2012).

Species with discrete breeding sites restricted by habitat may display genetic structure that could increase, and become inbred, with further habitat loss and climate change without immigration (Day et al., 2023). These changes may consequently lead to their rapid decline if survival is also low (Schaub et al. 2012, 2013). Understanding how these populations are connected through immigration and emigration (e.g. as in le Roux & Nocera 2021 using Motus on Chimney swifts) to avoid loss of genetic diversity, is important for deciding what conservation measures might be useful (Driscoll et al. 2014). We can estimate emigration and immigration rates of a species of interest, through comprehensive tagging campaigns (ethical considerations of such projects notwithstanding; Soulsbury et al. 2020), where Motus stations cover initial breeding sites, and at the same time the potential areas to where the birds might disperse.

Regional scale movements of juvenile Blackpoll warblers (*Setophaga striata*), Kirtland's Warbler and Barn Swallow (*Hirundo rustica*), have been demonstrated prior to migration using the Motus network (Brown and Taylor 2015, 2017; Evans 2018; Cooper and Marra 2020). Data are particularly needed from juveniles to assess when, how and why they decide on breeding site settlement (Doerr and Doerr 2005; Mukhin et al. 2018), and these studies suggest that tracking the dispersal of breeders, and fledging juveniles, to new habitats in the region, is feasible using this system.

Questions remain about the function of exploratory dispersal movements, which may be preparatory information gathering trips (‘homing target’ or ‘habitat optimization’ hypotheses, Mitchell et al. 2015), or pre-migratory flights (Züst et al. 2023). This exploration may also relate to range expansion, and individual or species responses to climate change (Driscoll et al. 2014, Dufour et al. 2021, 2022). Tracking individuals during the dispersal phase can help us to understand the role of (long-distance) dispersal in the evolution of new migration routes and wintering grounds, perhaps as part of the wider phenomenon of vagrancy (Lees & Gilroy 2009, Dufour et al. 2021, 2022).

Motus’ ability to expand spatially and temporally beyond the capabilities of manual VHF tracking, thus reducing bias and monitoring ‘hidden’ movements (Züst et al. 2023), can then increase the power of both juvenile fledging studies (Cox et al. 2012), and medium-long distance post-breeding dispersal (Evans et al. 2018, Hayes et al. 2024). Results from such studies can benefit practical conservation decisions to improve our understanding of how far and in what direction juveniles disperse. Tracking of many different young individuals can also highlight how individual phenotypes and differences in body condition might lead to differential post-fledging survival (Motus fledging study of barn swallows: Evans et al. 2020), and how this might be affected by surrounding habitat quality (Wood thrush: Hayes et al. 2020). These practical elements are invaluable to formulate effective conservation measures and facilitate population stability (Travis and Dytham 2013; Niebuhr et al. 2015, Endriss et al. 2019).

Understanding migratory decisions

In addition to using the Motus network to describe migration, it can facilitate an 'experimental' approach, i.e. extending laboratory-based studies in natural scenarios (Goymann et al. 2010 and Schmaljohann and Klinner (2020). For instance, by radio-tagging "lean" and "fat" individuals of a species on a single day to minimize the effect of weather variation on the birds' departure decision (e.g. Karwinkel et al 2022, 2024). When numerous individuals subject to the same external conditions are tracked at the same time, this may then allow estimation of conditions when most individuals migrate (Delingat et al. 2008, Schmaljohann & Klinner 2020), for example during favourable winds (Lagerveld et al. *In Press*).

Parameters derived from flights of individuals tracked with Motus such as departure and landing decisions, speed and routes (Figure 5a; Brust et al. 2019, Packmor et al. 2020, Brunner et al. 2022; Linhart et al. 2023, Ruppel et al. 2023), can allow comparisons in behaviour among individuals of different populations, and those that orient across and around barriers (Figure 5b; Schmaljohann & Naef-Daenzer 2011, Woodworth et al. 2015; Brust and Hüppop 2022). An improved understanding of migration behaviour, its limitations and flexibility among different species, can help us to better predict how species might adapt to changes around them and improve efforts towards their conservation (Sutherland 1998).

Obtaining individual responses to environmental stressors

Motus can also address identifiable conservation concerns, and detect responses to specific forms of anthropogenic or environmental disruption. Anthropogenic structures, such as offshore wind turbines, can attract migratory birds, potentially causing increased mortality through collision (Perrow 2019) or evoke avoidance behaviour leading to increased, delayed, fitness costs due to longer routes and higher energy expenditure (Schwemmer et al. 2023). Such impacts are still largely unquantified on migratory populations of birds (Marques et al. 2021). One possibility is to use Motus in combination with acoustic monitoring (as in Lagerveld et al. 2023), whereby we can localise the interaction of tracked individuals with near- and offshore infrastructure, and contextualise these known individuals amongst con- and allospecifics, detected by the acoustic recorders (Loring et al. 2019, Willmott et al. 2023).

Other anthropogenic disruptors are (agro-) chemicals such as neonicotinoids, which can impair the progress of migration in different taxa (Cabrera-Cruz et al. 2020). Eng *et al.* (2019) used Motus tracking to show responses to neonicotinoid ingestion by White-crowned sparrows (*Zonotrichia leucophrys*), whereby migrating birds on stopover are severely impaired in their ability to fuel, despite significantly increasing the length of stopover.

Further, artificial light at night (ALAN) has been shown to attract night-migratory birds to bright, often urban, areas (McLaren et al. 2018, Smith et al. 2021, Horton et al. 2023). These areas may act as potential ecological traps (i.e., inadequate stopover sites that might present higher risk of mortality; Van Doren et al. 2021). Similarly, anthropogenic electromagnetic radiation (‘electrosmog’) has been shown to disrupt the magnetic compass of night-migratory songbirds (Engels et al. 2014). As this was observed in the lab environments with caged birds, it poses the question whether ‘electrosmog’ is also a hazard for freely moving birds in the wild. Here we can apply Motus tracking, where directional and time to depart data can be collected by local and regional arrays of receivers positioned in and around areas of high urban density.

Combining Motus tracking with physical samples

Simultaneously collecting samples (e.g. feathers, saliva, blood or faeces) that tell us something about the physiological state of the animals, together with movement behaviour, can help us better understand how the physiology of an individual influences its migratory decisions. The high temporal resolution of tracking with Motus now allows us to link physiological indicators, especially those changing rapidly (e.g. hormones), much closer to their movement (e.g. Eikenaar et al 2020). This could for example include site quality, by correlating stopover duration and habitat use, as recorded by Motus, with body condition and immune function (Schmaljohann & Naef-Daenzer 2011, Hegemann et al. 2018, Brust et al. 2022). This would allow us to understand whether the sites provide the necessary functions for stopover required by migrants. If not, targeted conservation measures could be taken to restore the missing functions.

Genetic analyses in conjunction with recorded migratory behaviour (direction and routes, which are accessible with the high spatiotemporal accuracy of Motus), could indicate population-specific differences and possible significant regions in the genetic structure that are important for the genetic coding of migratory behaviour (Ruegg et al. 2014, Bossu et al. 2022, Sharma et al. 2023). Blood and faecal samples could be used to monitor the prevalence of pathogens that can be linked to body condition, population origin and subsequent migration decisions (ideally seasonal migration success; Neima et al. 2020, Morales et al. 2022). In the long term, standardised studies of migratory behaviour combined with sampling of tagged individuals could allow predictions of responses to global climate and habitat changes (Saura et al. 2014, Anderson et al. 2019).

Practical next steps: the logistics of developing Motus for flyway level research

Achieving greater geographical, i.e. near-continental, coverage of the Motus network stations is underway. However, this requires a strategic placement plan, cf. Lefevre and Smith (2020), based around the key questions discussed in this essay, and the special physical features of European landscapes (Figures 4, 5). The network will require significant capital investment and a collaborative spirit amongst researchers, conservationists and volunteers alike, because this task is too big for single groups.

Single groups can realize regional-scale networks through discrete projects which is a necessary way of completing a continent-wide network (Taylor et al. 2017, Griffin et al. 2020). Ideally, such projects fill in geographical gaps based on species ecology and migratory behaviour already garnered from other technologies (e.g. geolocators; Bayly et al. 2018, or radar; Robinson 2023). As well as capital, the development of the network will require significant time and focus to maintain equipment and retrieve data, particularly in remote areas. Such receivers are less likely to be monitored remotely because of signal and power restrictions, and therefore greater logistical efforts are required to obtain the stored data and undertake maintenance.

Cost per receiver can be realised for as little as €3000 - 5000 (~ four directional antennas, Sensorgnome receiver), but may approach €10000 dependent on requirements for installation and precise configuration of antennas. Each tag, whether from CTT or Lotek, is approximately €200, although this approaches €300 for the very smallest models. While cheaper than large, satellite enabled tags, this does not approach the low cost of metal or colour rings that allow researchers to capture and mark many thousands of birds. Cost reduction is hampered by limited market competition and a lack of open-source development, which contrasts the collaborative nature of Motus entirely, and must be addressed going forward to allow tagging on a much larger scale.

Lastly, the amount of data collected from Motus is enormous and is likely to continue to grow alongside other biologging data (López-López 2016), so appropriate statistical tools will need to continue to be developed. Complex Bayesian modelling frameworks to appropriately analyse Motus data have been developed, and tested in limited circumstances, e.g., modelling movement offshore (Cranmer et al. 2017; Baldwin et al. 2018), and estimating flight heights (Lagerveld et al. *In press*). Extending the applicability of these methods and developing integrated frameworks with multiple data types would enable researchers to make better use and further inferences about migratory parameters that can inform conservation (Gregory et al. 2023).

These challenges can only be solved in the long term, with a coordinated, international, collaborative effort, to develop joint funding applications and to work together for the benefit of the wider Motus community. This community must contain academics, policymakers, government officials, conservationists, amateur biologists and ecologists, who can develop well-defined, focused study objectives. The involvement of a diverse number of stakeholders is required, not just to share the cost burden and coordination responsibilities, but also to ensure fair data sharing, and the direct integration of such data into policy and conservation actions (UNEP 2020, Gregory et al. 2023; Guilherme et al. 2023).

Final Outlook

In this time of rapid ecosystem disruption, it is vital to work collaboratively to conserve migratory species. We need to work at multiple scales to answer questions about how species are confronting environmental changes. Motus can provide multi-scale data on the movements of bird without the need for recapture, even on species as small as Nathusius pipistrelles *Pipistrellus nathusii* (Bach et al. 2022, Briggs et al. 2023, Lagerveld *et al. In Press*), Yellow-browed warbler *Phylloscopus inornatus*), and large insects, such as the monarch butterfly (Knight et al. 2019, Wilcox et al. 2021). Motus' features and capabilities make it an attractive and exciting prospect for exploring as yet unanswered ecological, evolutionary, and behavioural questions.

There is a significant amount of logistical and planning work to develop and grow the network to reach its full potential in terms of basic and applied science, but such efforts that also focus on expanding the collaboration between parties, and realizing developed conservation strategies will result in benefits for birds, nature as a whole and ultimately, by supporting the One Health approach, us as humans.

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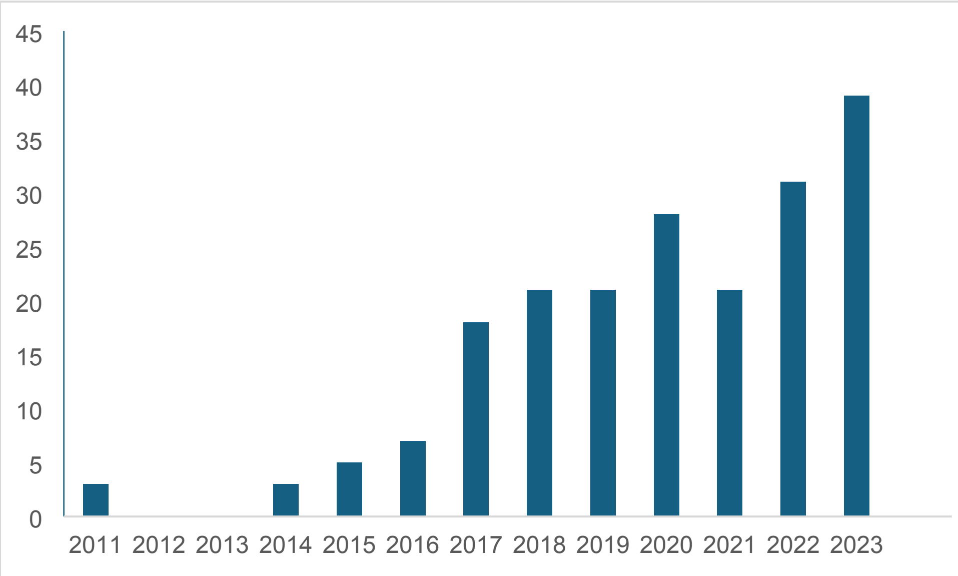

Figure 1: Number of publications per year (2011 – 2023), resulting from Motus data.. Source: motus.org

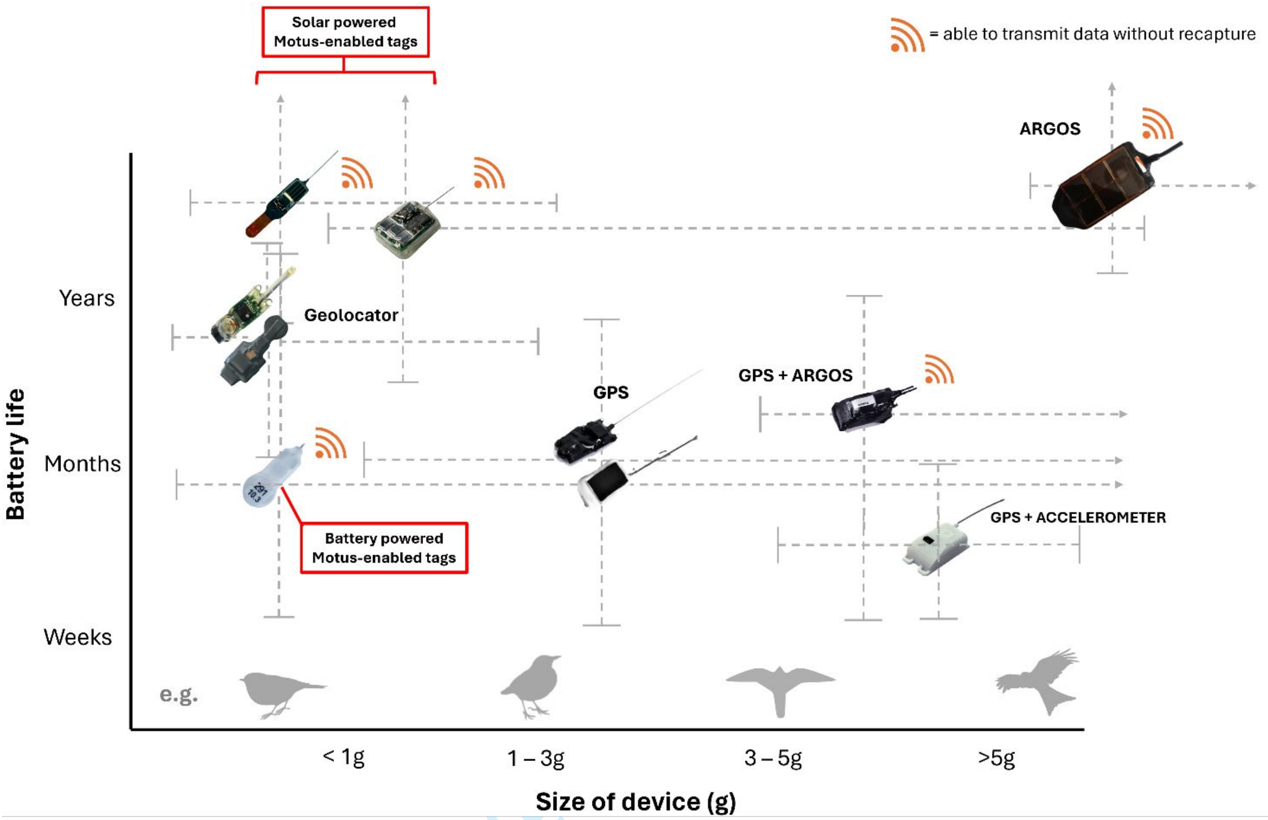

Figure 2: Capability and context of tags enabled for Motus. Icons indicate tag types and are positioned approximately in relation to their mean battery lifetime and size. Grey dotted lines represent variation on both axes taking into account programming influence on battery life and differences among and between device types. Orange 'wifi' symbols represent transmission capability, independent of the bird´s return to a specific location.

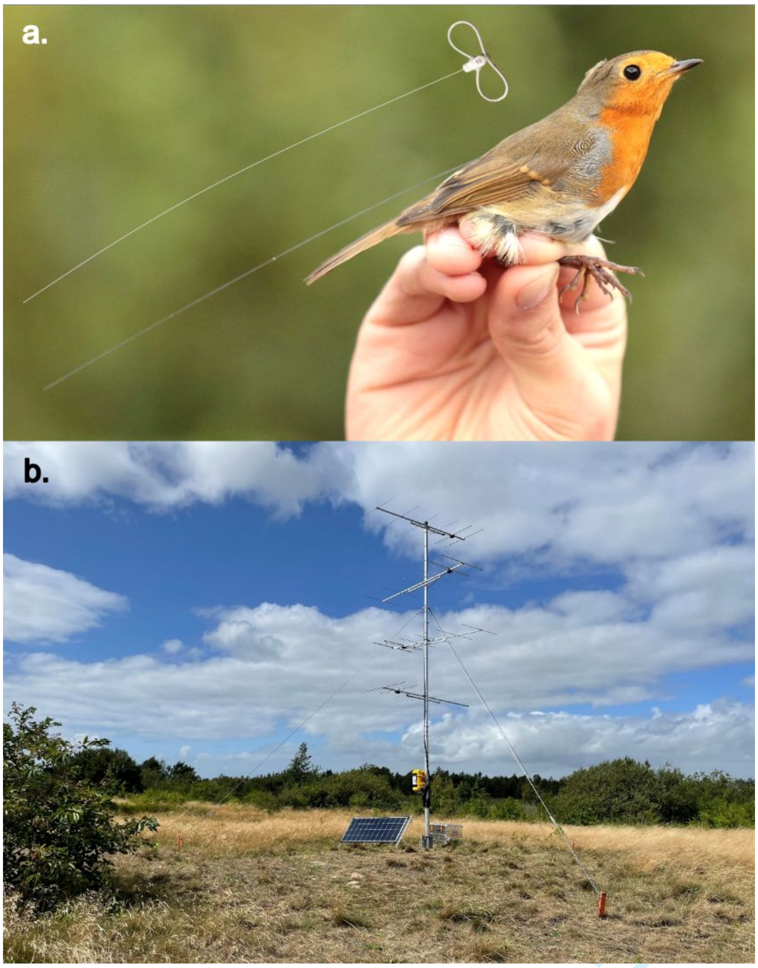

Figure 3a. European Robin (*Erithacus rubecula*) with attached radio transmitter with radio transmitter and attached leg-loop harness illustratively shown above the bird; b. a Motus receiving station (6 metre height), with 4 six-element-Yagi antennas pointing in four directions. The station is powered by solar, with a buffer battery (in aluminium box on ground). The electronics are installed in the small yellow box at the pole. Detailed information about tagging animals and building stations can be found at the Motus Webpage (motus.org/resources/) and from the regional Motus coordinators (motus.org/groups/regional-coordination-groups/). Photos: T.K.

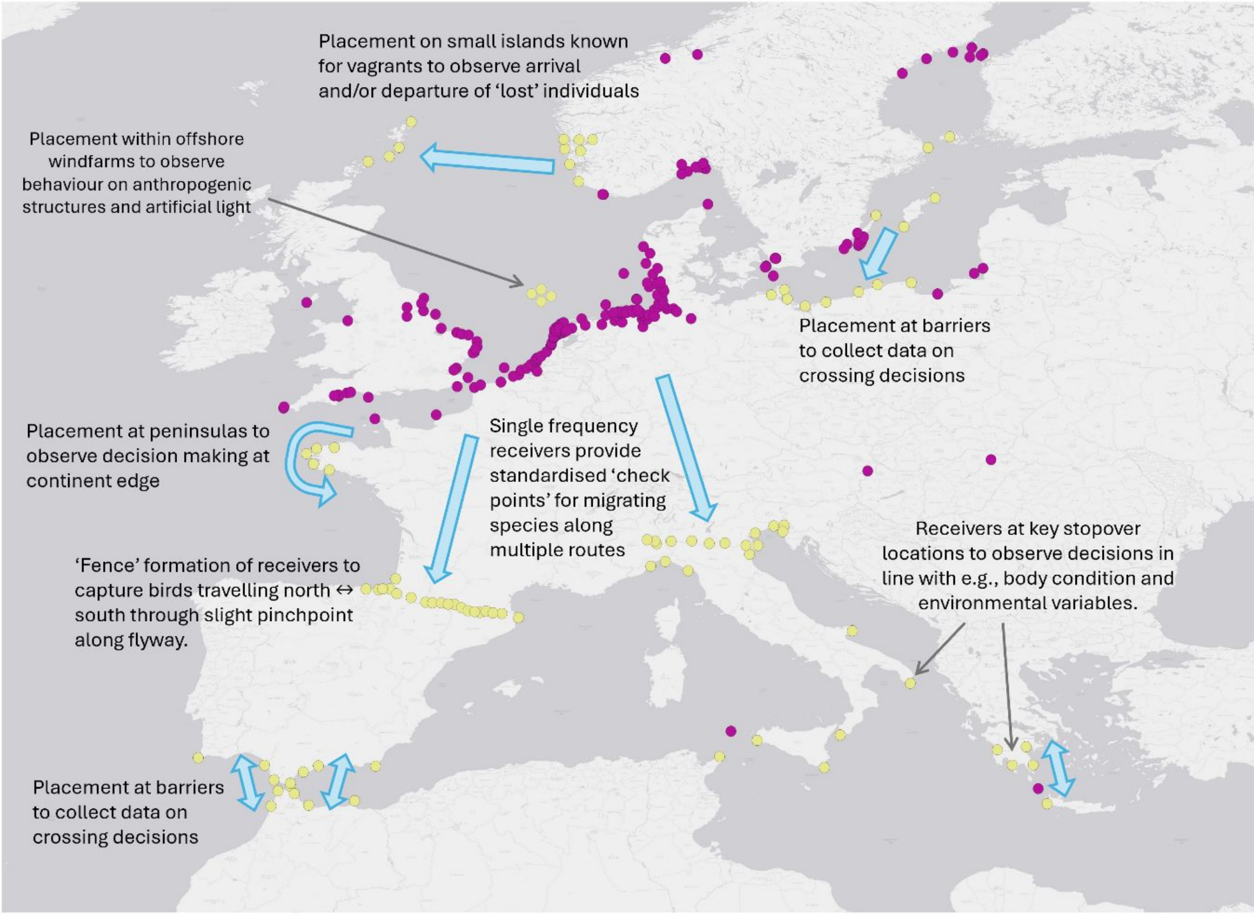

Figure 4: Current Motus receiving station network (purple dots) across the European continent, along with hypothetical future stations (yellow dots) to demonstrate potential to answer demographic and conservation-focused questions about bird migration. Blue arrows highlight flyways and movements of particular study interest.

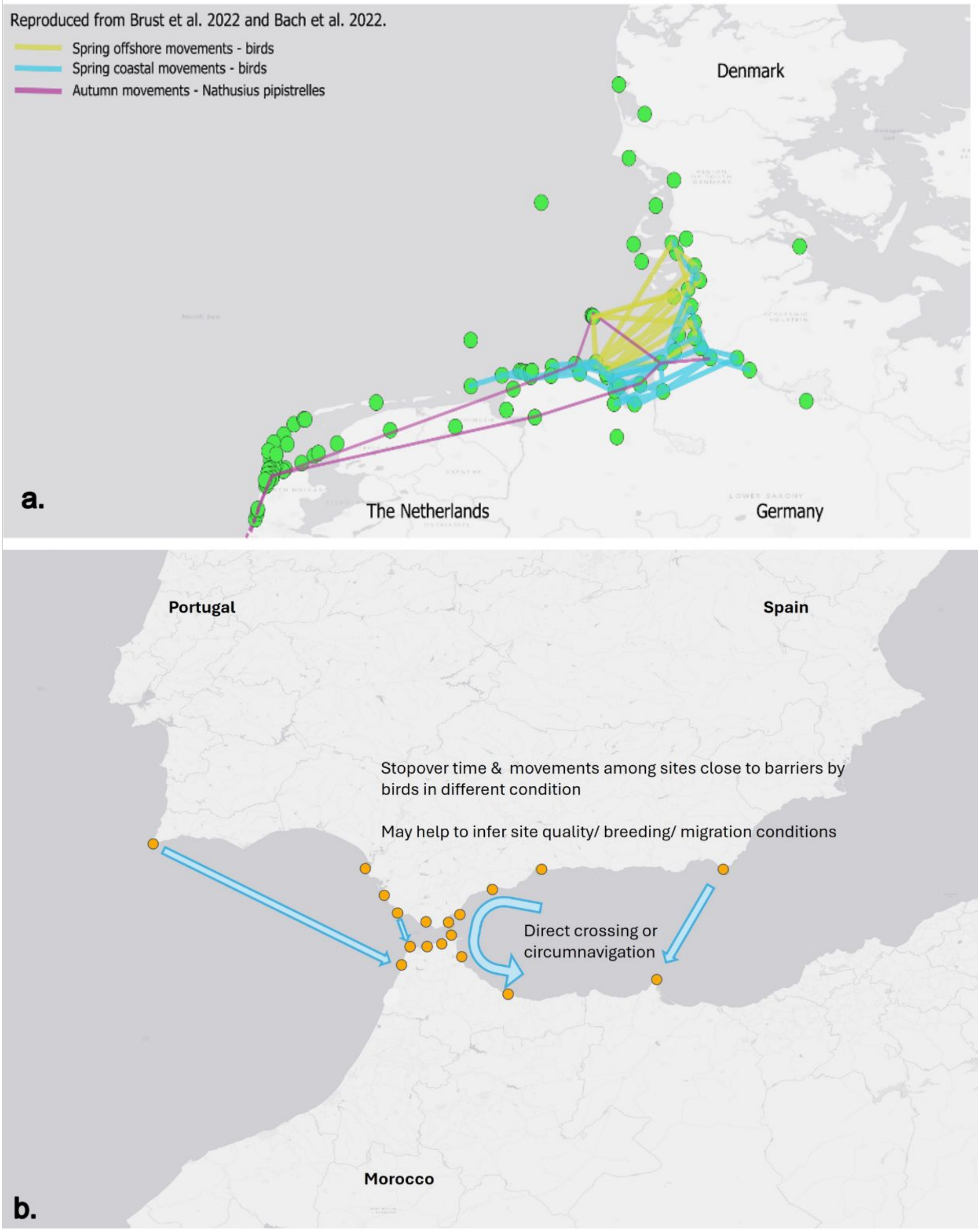

Figure 5: Studying behaviour of migrating animals at barriers; a: currently operational receiving stations (green dots) along the North Sea coast, and examples of tracks collected from birds and bats; b: examples of potential station placement (yellow dots) and data collection at Gibraltar, Iberian peninsula, where many thousands of migratory species will cross an important migratory barrier, the Mediterranean Sea. Blue arrows exemplify expected flight paths that could be detected by the set-up.

Manuscript: "Mapping migratory routes: Avian conservation-focused opportunities for a pan-European automated telemetry network" (24-593.R1)

Response to reviewer comments

Reviewer: 1

Comments to the Author:

The authors have responded completely and well to all of our comments, rewriting substantially to address all of my points. I am happy with the revision, and appreciate the authors taking the time to respond so fully to the comments. The essay was fine to start with and is now much better – it is a useful and timely paper on advances in conservation related research.

Response: We thank the reviewer for re-reading our manuscript, and for their kind words on the paper. We valued the reviewer's comments highly, which have substantially improved the manuscript, and are very pleased that the reviewer agrees with our revisions.

Reviewer: 2

Comments to the Author:

The manuscript has been substantially improved from the previous round and the authors have properly addressed the comments of the reviewers. The language is still not the best and I am attaching the manuscript files with specific comments and suggestions of text edits.

Response: We thank the reviewer for their comments on our revised manuscript, and we appreciate their efforts and attention to detail in reviewing it. The reviewer has made some specific comments on the draft PDF, which we refer to below.

L56: We have added a comma after 'migratory timing' as suggested

L57: We have replaced 'stationary' with 'stopover', as suggested

L60: We have replaced 'status' with 'trends', as suggested

L68-69: We have replaced 'sufficient' and 'robust' with 'sufficiently high' as suggested

L84: We have removed 'such', replaced the '/' with 'and' and added 'that are at risk of decline', as suggested

L102: We have replaced 'are produced' with 'take place' as suggested.

L103 – 105: We have changed the structure of the sentence accordingly; we have replaced 'to hope to retrieve one recovery in sub-Saharan Africa, upwards of', with 'about' and then included 'for each recovery in sub-Saharan Africa' later

L126-128: We have removed the sentence on these three lines, as suggested

L129: We have included 'to track migratory birds' as suggested

L159-160: We have included a comma after 'still patchy', and removed 'where the data are most lacking' as suggested

L164 -165: We have removed 'the addition' and replaced with 'adding antennas', and then replaced 'of antennas to monitor' with 'for monitoring', as suggested

L165 – Comment: "please always have space between values and units, excluding percentages and degrees"

Response: We have added a space as suggested, and then double checked all other instances of units within the text.

L171: We have replaced 'not least' with 'including'

L172: We have removed 'improving its performance' as suggested

L173: We have replaced 'As well as' with 'In addition to' as suggested

L189: We have placed parentheses around the year of the reference

L192: We have replaced 'and' with 'resulting in' as suggested

L193: We have added 'across Europe' at the end of the sentence, as suggested

L195: We have added 'European' in front of 'birds', and replaced 'Studies in Europe are now beginning to understand more about' with 'including a better understanding of'

L197: We removed the redundant 'of' and replaced with an additional example: *and differences between long and short distance migrants in stopover time and flight direction (Rüppel et al. 2023b)*'

L201: We removed 'currently' as suggested

L202: We replaced 'population projections' with 'population studies' as suggested

L203-207 – Comment: Something is not quite right with this paragraph as you already mention above that motus can gather this data. Please edit possibly by deleting the second part of the sentence "can help us..." and moving it before the examples. Yet, the previous sentence is also not a good one to end the paragraph so it also need to be moved ot changed.

Response: We agree there is some repetition here, so we have edited as suggested, by deleting the sentence. We also deleted the previous sentence, and have also restructured the sentences on lines 199-202 to reflect the removal of the latter sentences.

L233: We have added 'the calculation of' as suggested

L239: We have added 'by' as suggested

L256: We have edited the sentence to be 'can help with elucidating the functions of stopover sites' as suggested

L263: We have edited the sentence to be 'when the current conditions of stopover sites may degrade, or they might even disappear completely' as suggested

Comment: This paragraph is made from three sentences. The first talks about how the use of motus can be helpful for understanding the functions of stopover. Then the second sentence suggests that the ID of these functions is important for future changes. The third sentence reports about a study that identified a stopover area used by two passerine species, suggesting that is should be conserved. The problem is that this last sentence only vaguely relate to the first two sentences as it doesn't describe stopover functions and future changes or degradation of the conditions. Please edit to make the text more coherent.

Response: We agree with the reviewer that the last sentence of the paragraph did not link as well as it could. We have edited – and split – the sentence, to explicitly highlight the stopover site's function as a refuelling location, important for long distance journeys.

L286: We have replace 'Juvenile and post-breeding' with 'Natal and breeding' as suggested

L287: We have added 'partly' as suggested

Comment: The last part of the sentence is coming out of the blue - you were discussing dispersal and now you move to the evolution of new migration routes and wintering locations - although related to dispersal to some extent, this is a topic that cannot just be mentioned without further explanation at the end of a paragraph dealing with dispersal. Please edit.

Response: We agree that the sentence is a little bit 'tacked on' and have changed the whole paragraph substantially, to reflect the removal of that section of the sentence. These lines have been moved elsewhere in the manuscript (to lines 310-312, and 320-323).

L297- Comment: Please revise the text, preferably split to two sentences

Response: We have revised as suggested, splitting the sentence after (Day et al., 2023).

L310 – Comment: I am missing here a concluding sentence that will connect the description of the last sentence to the concepts outlined earlier in the paragraph. For example:

These regional scale movements suggest that tracking the dispersal of breeders to new habitats in the region is feasible using this system.

Response: We agree that there is additional information needed here. As such, we have moved information that no longer fitted in lines 290-292, and added the reviewer's suggestion of new text at the end.

L330 – 338 Comment: Please split this extremely long sentence to at least two (maybe 3 is even better) sentence.

Response: We thank the reviewer for picking up on this, and have split the sentence as suggested into three parts; firstly on line 332, and again on line 336.

L363 – 368 Comment: not necessarily. This is an option to better understand some aspects that Motus cannot cover, but it is not a must

Response: We thank the reviewer for picking up on unclear language here, and have edited these lines to rephrase. To summarise our edits here, we wanted to say that this was just one possibility for trying to quantify impacts on populations, in terms of offshore interactions.

L438: We have replaced 'hundred' with 'thousands' as suggested

L456 Comment: I'm not sure that this community MUST include radio enthusiatics. If you think otherwise please justify. If not, please remove or lower the tone.

Response: We have removed this as suggested.

L457: We have added 'is required' after 'stakeholders' as suggested

L472 – 474 Comment: please revise the text by avoiding repeating the same word twice within the same sentence, as much as possible.

Response: We apologise for the repetition, and have revised the sentence to remove the second mention of 'grow the network'. It now reads '..but, such efforts that also focus on expanding the collaboration between parties, and realizing developed conservation strategies...'

Figure 1. Comment: Data for 2024 is probably misleading as some studies likely have not yet been counted in the motus website. Please end the graph in 2023

Response: We agree with the reviewer, and have removed the data for 2024 as suggested.

We would also like to highlight some further edits of mistakes we spotted whilst re-reading the text. This also includes edits to reduce the word count in order to meet the Essay criteria (5000 words). For example deletions on lines 193-195 (but displacement of one comment from here to 161-162); deletion of 206-209 as it was repetition; lines 213-214 as unnecessary; 389-390 deleted as repetition; line 419 deleted as repetition from sections above.

Mapping migratory routes: Avian conservation-focused opportunities for a pan-European automated telemetry network

Abstract

Accelerated biodiversity loss during the Anthropocene has destabilised functional links within and between ecosystems. Migratory species that cross different ecosystems on their repeated journeys between breeding and non-breeding sites are particularly sensitive to global change because they are exposed to various, often ecosystem-specific threats. As these bring both lethal and non-lethal population impacts, many migratory species are declining, making this group especially vulnerable to global change.

To mitigate their decline, research at a continental and flyway scale is required to adequately monitor changes in the migratory and demographic processes of populations during all parts of the annual cycle. The Motus Wildlife Tracking System (Motus) could provide a solution to data gaps that exist ~~particularly~~ for small, migratory species. Motus is an automated telemetry system for animal tracking, which provides a collaborative network by using a single VHF radio frequency for all tracked individuals, in combination with an individual tag identifier. Motus can provide information on movements made by individuals of small migrant species, thus aiding our understanding of aspects of their migration that could impact demographic parameters.

Here we describe conservation-focused research opportunities, with a particular lense on small European migrant birds. We highlight examples from the existing network, and identify geographical gaps which, if filled, could track continent-wide movements. We conclude that Motus is a useful tool to produce individual-level

migration information for a variety of small-bodied taxa, and that a drive to expand the network will improve its ability to direct conservation plans for such species.

Introduction

Biodiversity loss driven by land use change, exploitation of natural resources, and affected further by climatic disruption, is a defining feature of the Anthropocene (Sala et al. 2000). A decline in habitat availability and ~~significant~~ disruption to ecosystem structure, reducing critical services such as nutrient cycling, carbon storage and flood control , has led to declines in a wide range of taxa globally (Jaureguiberry et al. 2022). The impacts of anthropogenic development do not just manifest through physical changes, i.e. habitat loss, but also through increases in zoonotic and vector-borne diseases (Jaureguiberry et al. 2022), and pest outbreaks (Ayres and Lombardero 2018). These impacts affect species' distributions, abundances, fitness, and consequently their ability to complete their life cycle successfully (Bellard et al. 2012).

Of particular concern are migratory species, which serve as ecological indicators and ~~direct~~ providers of vital contributions to ecosystem functioning, including biomass production, pollination, and pest control (Bauer and Hoye 2014, Satterfield et al. 2020). Migratory species experience a variety of environmental conditions on their seasonal, sometimes inter-continental journeys (Turbek et al. 2018, Zurell et al. 2018; Horton et al. 2020; Howard et al. 2020). Rapid changes in land use and configuration, throughout their annual cycle, can mean that their requirements for reproduction and survival are compromised (Birnie-Gauvin et al. 2020, Marcacci et al. 2022, Rigal et al. 2023). There are also additional threats such as (illegal) hunting (Jiguet et al. 2019), the extension and complication of ecological barriers (Gauld et al. 2022), as well as increasingly unpredictable climatic patterns decoupling the phenology of ecologically linked species (Iler et al. 2021, Clarke et al. 2022).

These challenges directly conflict with the multi-factorial optimisation of migration, which is often based on inherited, integrated migration strategies (Åkesson and Helm 2020; Schmaljohann et al. 2022, Fattorini et al. 2023). While migrant species differ in their migratory timing, distance, speed, and route, their journeys all involve repeated, alternating migratory endurance flights and ~~stationary~~ stopover periods for resting, recovering and fuelling (Alerstam et al. 2003; Åkesson and Hedenström 2007; Schmaljohann et al. 2022). Understanding the factors impacting population ~~status~~ trends of these species, i.e., the changes in vital rates that drive population growth or decline, is essential (Morrison et al. 2016), as many migratory species cannot respond to changes at a sufficiently rapid pace, producing widespread population declines (Both et al. 2006, Wilcover & Wikelski 2008, Frick et al. 2020, Rosenberg et al. 2019, Vickery et al. 2023).

The Convention on the Conservation of Migratory Species highlights the need for a multi-species, flyway level perspective in terms of research into population declines (UNEP/CMS 2020, Frick et al. 2020, Marcacci et al. 2022, Chowdury et al. 2023, Vickery et al. 2023). However, gathering ~~sufficient~~ data from a ~~robust~~ sufficiently high number of individuals from different populations at this scale, is extremely challenging (Morrison et al. 2016; McKinnon and Love 2018), ~~. Research at a flyway scale is complicated~~ and reliant on international collaboration (Nadal et al. 2020; Vickery et al. 2023, Serratosa et al. 2024). ~~,~~ P~~p~~articularly for small and light migratory passerines, waders and highly aerial species such as swifts, whose size and behaviour have rendered it difficult to study their movements (Wikelski et al. 2007, Fiedler 2009).

Current methods and their limitations

Studying when and where differences in population processes occur in migratory birds is notoriously difficult (Doerr and Doerr 2005; Border et al. 2017, Telensky et al. 2020)~~, and hampers our understanding of the population dynamics in such species~~. However, quantifying variation in survival, mortality, emigration and immigration (summarized as dispersal), is crucially important to formulate effective conservation measures for ~~such~~ populations and ~~/~~species that are at risk of decline (Gómez et al. 2021, DeMars et al. 2023).

Currently, we have little detailed spatial and temporal information on migrating small birds. Broad scale migration patterns across Europe, including concentrations of both avian and insect migrants passing through marine and mountainous regions, have been identified using radar (Bruderer & Jenni 1990, Bruderer & Liechti 1999, Nilsson et al. 2019, Weisshaupt et al. 2021, Hirschhofer et al. 2024). Yet radar data largely do not allow us to tease out species-specific and individual-level variation in large-scale movements (Schmaljohann et al. 2008, Zaugg et al. 2008), which would facilitate links to demography, physiology and ecology.

In contrast, several million individuals have been marked using metal or colour rings across Europe (Du Feu et al. 2016, Spina et al. 2022), contributing to our fundamental knowledge of bird movements. Yet recapture, recovery, and resighting probabilities are largely low (across 32 European level ringing schemes, recovery rate for *all species combined* varied from 0.6 – 7.6%; Baillie 1995). This is particularly the case on the wintering grounds but is highly variable amongst species and locations (Thorup et al. 2014). For example, the Willow Warbler (*Phylloscopus* trochilis) is ringed in huge numbers on its breeding ground in northern Europe, but only a very small number of recoveries ~~are produced~~ take place in Africa.~~;~~ ~~s~~Specifically, in Finland, ~~to hope to retrieve one recovery in sub-Saharan Africa,~~ ~~upwards of~~ about 16000 individuals of this species ~~-~~needed to be ~~marked~~ ringed on the breeding grounds for each recovery in sub-Saharan Africa (Hedenström and Pettersson 1987).

~~Many of~~We can the disadvantages of these ~~aforementioned~~ methods ~~can be addressed~~ by tracking individual migratory, ~~movements. There are also other biological processes whose elucidation would benefit from individual tracking, including~~ pre- and post-breeding dispersal (Mukhin et al. 2005, Züst et al. 2023), and nomadic, non-breeding movements (Snell et al. 2018; Mckinnon et al. 2019). However, individual tracking of small migrants requires tracking devices weighing a maximum 3-5 % of an individual's body weight (Barron et al. 2010), which excludes most tracking technology on the market (Figure 1; Bridge et al. 2011, McKinnon & Love 2018), including new low-power, wide area devices such as SigFox or LoRaWAN (Wild et al. 2023). Radio- transmitters, however, have already reached minimum weights of currently 0.13 g (Lotek NanoPin), lighter than the smallest light-level geolocators (Lotek: 0.3 g), and significantly smaller than GPS units which require significant energy to relay information to a satellite and fix a position. Some radio-tracking systems, e.g., the tRackIT System and the ATLAS project, have narrow spatial coverage and a limit on how many individuals (c. 200) they can monitor concurrently (Gottwald et al. 2019, Beardsworth et al. 2022).

The Motus Wildlife Tracking System (Motus) exploits a network of VHF receiving stations aligned on the same frequency, which continuously receive and record uniquely-coded signals of tagged individuals using mostly directional Yagi antennae without the need for recapture (Taylor et al. 2017, Imlay et al. 2020).

~~In this essay we focus on migratory birds, primarily passerines, as the additional information gain of Motus is most recognisable for this group compared with previous work, than in the other two taxa.~~ Here, we focus on filling conservation and demographic-specific knowledge gaps using Motus to track migratory birds, and we hope to further spark the collaborative spirit of Motus to create a denser network in Europe and resemble the situation in North America.

Motus and its benefits

Motus originated in Canada as a partnership between Acadia University and Birds Canada (Taylor et al. 2011, 2017), and its spread across the Americas is a great success story of collaborative research (see https://motus.org). Globally, to date (~~mid-October~~December 2024) there are now ~~860~~ 916 established tagging projects, which combined have tagged ~~49, 895~~50,668 animals of ~~397~~ 402 species. The entire Motus network at the moment consists of ~~2081~~ 2060 receivers, and the largest single project array consists of 109 receivers in Ontario.

Publications resulting from Motus data total 213, which combined were cited according to Zotero >500 times. The number of publications based on Motus data has more than doubled since 2015/16 (Figure 2), and the lead and coauthors of these publications are rarely just limited to academics; the application of Motus has been recognised by multiple stakeholders such as the US Fish & Wildlife Service (USFWS), National Parks Service (NPS), Canadian Wildlife Service (CWS) and BirdLife Europe (Machado et al. 2024).

Investment in the network across North America continues to grow, including in March 2024 a grant of $3.1 million CSD awarded to a consortium of five Canadian universities and Birds Canada to continue installing Motus receiving stations across the country, as well as to invest in community-based science. This investment, combined with a specific mention within the CMS of automated radio tracking deployed at a flyway scale (COP13, Resolution 12.26) demonstrates the value, and potential future value, of Motus to conservation.

The initiation of Motus in Europe started in 2017, and although the network has grown slower than in the Americas there is now a dense network of passive receiving stations (e.g. Figure 3) along the coasts of Germany, the Netherlands, and the UK, and to a slightly lesser extent in Sweden, Denmark, Belgium and France, with a number of additional stations in other countries, and offshore (Figure 4).

The network of stations in Europe is still patchy, particularly ~~where data are most lacking~~ in eastern Europe, and there is a lack of a universally-permitted tracking frequency, so ~~it~~ does not yet allow continuous tracking across the continent. In many European countries, the frequency of 150.1 MHz is authorised either temporarily or permanently for wild animal telemetry tracking. Multi-frequency detection by Motus receivers is possible, but it incurs additional expense for extra equipment. For example, ~~the addition~~ adding antennas to receiving stations ~~of antennas to~~ for monitoring the license-free frequency of 434 MHz would cost approximately €80 – 300 per station, for an additional 1 - 4 antennas, plus the extra cost of cables. For the tags, researchers are able to select from among a number of options and device parameters, including burst interval (usually from 1 s to 1 min), battery or solar power, attachment and antenna type, in line with their specific scientific requirements (Figure 1).

Motus has many promising features,~~ not least~~ including its extended temporal and spatial data gathering capacity, ~~improving its performance~~ compared to standard radio-tracking. ~~As well as~~In addition to autonomous, near-real-time recording of the receivers and sub-0.5 g tags, the spatial scale of detections is in the order of several kilometres, rather than orders of magnitude higher as with geolocators (Taylor *et al.* 2017), although new multi-sensor tags have shown substantial improvements in positional accuracy (Nussbaumer et al. 2023). Receiving stations can, in theory, be placed anywhere (see Figure 3b) and have a 10 kilometre-plus detection range, and therefore data capture is less limited by researcher effort, in contrast to commonly used methods such as bird ringing (Griffin et al. 2020; Flack et al. 2022). Fixed positioning of the receiving stations (ideally ~~located~~ at sites of importance to the species of interest to maximise detection probability), along with an unrestricted recording period, also enables standardized data collection, reducing observer-bias (Griffin et al. 2020).

Despite the advantages, ~~we have to be aware of the~~ there are drawbacks of radio-tracking studies in general. Most studies do not detect all of the individuals which are tagged; the reasons for this are many and are not mutually exclusive, but can include loss of the tag, predation, emigration, tag failure, topography or weather conditions. Crewe et al. (2020) reported rates closer to 50-70%, whereas a dense coverage of receivers on the small island of Helgoland repeatedly resulted in detection rates of 95-100% (Karwinkel et al. 2022, 2024). ~~And, unlike in North America, there are many different countries and stakeholders involved and a lack of a universally permitted frequency for animal tracking in the wild.~~ There are also uncommon occurrences of high levels of 'false positive', or uncoded detections, which can appear if large numbers of individuals are released at once close to a receiver (reference). Mitigations, such as staggered switching on of the tags to encourage differential pulse emission, can be put in place, and the numbers required to cause this confusion mean this is unlikely to happen in a ‘natural’ scenario.

Motus is already producing important insights into the movements of migrating and wintering European birds, including a better understanding of~~. Studies in Europe are now beginning to understand more about~~ the migratory and pre-migratory movements of sea-crossing thrushes (Brust et al. 2019) and differences between long and short distance migrants in stopover time and flight direction (Packmor et al. 2020, Rüppel et al. 2023). ~~and of~~. Examples from Europe and North America show that Motus can gather long-term, annual cycle data, in a relatively low cost manner, on groups and time periods (e.g. juvenile fledging) that are ~~currently~~ often missing from population ~~projections~~ studies (Satterfield et al. 2020, Martell et al. 2023).~~, and necessarily require long-term, broad spatial scale, annual cycle data collection (Satterfield et al. 2020~~). ~~Yet, funding, time, and staff resources, and the vast areas over which migration may occur, make collecting the necessary data difficult (Lefevre and Smith 2020). Motus, as a relatively low-cost, collaborative, spatially dispersed array of receiving stations, can help us in gaining those data (Taylor et al. 2017).~~

How Motus can help to address knowledge gaps in small migratory bird movement by collecting demographic information.

~~In the following sections, we address how demographic processes and further important information can be obtained using Motus.~~

Survival and mortality

Despite the biological significance of survival and mortality on population size and its dynamics (Sandercock 2020), little is known about both rates in migratory passerines. Within migratory species, variation in survival among populations can be linked to alternative routes and their different pressures (Hewson *et al.* 2016). The latter may increase population-specific immediate and delayed fitness costs (Dhanjal-Adams et al. 2017), which might be particularly prevailing in those areas that support high numbers of ‘co-migrants’ (multiple species moving through major sites and corridors simultaneously – Cohen et al. 2020). The convergence of otherwise spatially segregated populations at single locations may also increase the probability of disease transmission with delayed fitness costs (Cohen et al. 2020).

To obtain information on route- or area-specific mortality rates, focusing receiving station placement in closely-packed ‘fence’ or ‘curtain’ formation (Figure 4) would provide ‘checkpoints’ for tagged migrants along their migratory routes. If there are sufficient stations intersecting migratory routes (and adequate numbers of individuals are tagged), then obstacles that slow down migration can be identified, alongside estimates of mortality rates for such areas (Klaassen et al. 2014, Buechley et al. 2021). Survival has been successfully estimated using Motus for the Kirtland’s warbler *Setophaga kirtlandii* (Cooper et al. 2024). This species’ limited population size and discrete wintering range, lends itself to Motus, and a robust design Cormack-Jolly-Seber model allowed <u>the calculation of</u> apparent survival rates ~~to be calculated~~ with a high level of certainty, knowing that a high proportion of marked individuals had been detected.

Gonzalez et al. (2021) used Motus to identify habitat-specific overwinter survival rates in the Swainson’s Thrush (*Catharus ustulatus*), which can be used to inform habitat protection and management on the wintering grounds. Motus has also been used by Brunner et al. (2022) to identify high migratory connectivity amongst populations of the elusive Swainson's warbler (*Limnothlypis swainsonii*), which has implications for population-specific changes and can direct future monitoring work. These cross-continental studies demonstrate the power of Motus to collect data at multiple scales, helped by the fact that tags do not need to be recaptured to retrieve the data, therefore reducing bias. Extensive testing of detection capability of an antenna array in a fixed area, is essential to maximise coverage and the ability to produce survival estimates. Better still if survival is estimated across a limited area (Cooper et al. 2024) and restricted temporal period to increase the robustness of the estimates (Evans et al. 2020, Bliss et al. 2020).

Identification of Stopover sites

Motus can be used in regional arrays that expand outwards from a known stopover site, allowing identification of exploratory and regional movements by birds that may be assessing the wider area, often undertaken at night (Taylor et al. 2011, Brown and Taylor 2015, Schmaljohann & Eikenaar 2017). In Europe, this could build on current ringing efforts at hotspots (e.g. Bay of Biscay; Strait of Gibraltar) but at spatial scales not feasible for ringing. Pinpointing specific sites for targeted conservation efforts is important, where limited, localised stopover site use could induce higher vulnerability in certain migrating species (Bayly et al. 2013, Gómez et al. 2014, Hagelin et al. 2021).

Temporal information on arrival and departure time, using Motus on multiple individuals of different species, can help ~~to~~ with elucidating the~~e~~ functions of stopover sites (Moore 2018, Linscott and Senner 2021, Schmaljohann et al. 2022). Identification of these functions could be very valuable in the context of future global climate change, when~~re~~ ~~stopover sites'~~ the current conditions of stopover sites may degrade, or they might even disappear completely (Bayly et al. 2018). Smetzer and King (2018) used a regional Motus network to identify a major stopover area for Blackpoll warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceous*) ~~at~~ in the Gulf of Maine of the United States.~~,~~ ~~to identify a major staging area for Blackpoll warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceous*),~~ The prolonged stopovers recorded by both species suggest that the region may serve as a major refuelling area when preparing for long-distance migratory endurance flights, thus demonstrating the area's high conservation value.

Stopover sites on either side of ecological barriers, could be equipped with Motus stations in high densities, (e.g. distance of 5 - 10 km between stations but variation in detection distance due to topography and the behaviour of the species must be taken into account), to provide insights into how birds respond to such barriers (e.g. Sjöberg et al. 2015, Zenzal et al. 2021). This might include local to regional scale movements before crossing, intrinsic and extrinsic conditions required for a successful crossing, stopover duration, departure directions, and potential differences between populations and seasons. Both Holberton et al. (2019) and Herbert et al. (2022) used Motus to demonstrate site-based variation in stopover duration, which was related, at least in part, to bird condition and morphology. This indicates some level of migratory connectivity, ~~(such as Brunner et al. 2022),~~ and as such, loss or degradation of one or more stopover sites could have population level implications.

Dispersal, immigration and emigration

~~Juvenile~~ Natal and ~~post-~~breeding dispersal are critical but understudied fundamental biological processes, partly because nestling and juvenile survival is generally so low that high manpower and financial investment is required to track a few individuals. Dispersal consists of the initial process of emigration from a breeding site, and the subsequent immigration to another (Matthysen & Clobert 2012). ~~Data are particularly needed from juveniles to assess when, how and why they decide about breeding site settlement (Doerr and Doerr 2005; Mukhin et al. 2018), and to understand the evolution of new migration routes and wintering locations (Dufour et al. 2021, 2022).~~

Species with discrete breeding sites restricted by habitat may display genetic structure that could increase, and become inbred, with further habitat loss and climate change without immigration (Day et al., 2023).~~,~~ These changes may consequently lead ~~potentially leading~~ to their rapid decline if survival is also low (Schaub et al. 2012, 2013). Understanding how these populations are connected through immigration and emigration (e.g. as in le Roux & Nocera 2021 using Motus on Chimney swifts) to avoid loss of genetic diversity, is important for deciding what conservation measures might be useful (Driscoll et al. 2014). We can estimate emigration and immigration rates of a species of interest, through comprehensive tagging campaigns (ethical considerations of such projects notwithstanding; Soulsbury et al. 2020), where Motus stations cover initial breeding sites, and at the same time the potential areas to where the birds might disperse.

Regional scale movements of juvenile Blackpoll warblers ~~(*Setophaga striata*)~~, Kirtland's Warbler and Barn Swallow (*Hirundo rustica*), have been demonstrated prior to migration using the Motus network (Brown and Taylor 2015, 2017; Evans 2018; Cooper and Marra 2020). Data are particularly needed from juveniles to assess when, how and why they decide on breeding site settlement (Doerr and Doerr 2005; Mukhin et al. 2018), and these studies suggest that tracking the dispersal of breeders, and fledging juveniles, to new habitats in the region, is feasible using this system.

Questions remain about the function of ~~such~~ exploratory dispersal movements, which may be preparatory information gathering trips (‘homing target’ or ‘habitat optimization’ hypotheses, Mitchell et al. 2015), or pre-migratory flights (Züst et al. 2023). ~~It is unclear how t~~This exploration may also relate to range expansion and individual or species responses to climate change (Driscoll et al. 2014, Dufour et al. 2021, 2022). Tracking individuals during the dispersal phase could potentially help us to understand the role of (long-distance) dispersal in the evolution of new migration routes and wintering grounds, perhaps as part of the wider phenomenon of vagrancy (Lees & Gilroy 2009, Dufour et al. 2021, 2022).~~, but as these often occur at night (Schmaljohann et al. 2011), they are missed by many methods. As Motus can monitor an area of many kilometres wide, 24 hours a day, these movements should not be missed.~~

Motus’ ability to expand spatially and temporally beyond the capabilities of manual VHF tracking, thus reducing bias and monitoring ‘hidden’ movements (Züst et al. 2023), can then increase the power of both juvenile fledging studies (Cox et al. 2012), and medium-long distance post-breeding dispersal (Evans et al. 2018, Hayes et al. 2024). Results from such studies can benefit practical conservation decisions to improve our understanding of how far and in what direction juveniles disperse.~~,~~ ~~and~~ Tracking of many different young individuals can also highlight how individual phenotypes and differences in body condition~~-~~ might lead to differential post-fledging survival (Motus fledging study of barn swallows: Evans et al. 2020), and how this might be affected by surrounding habitat quality (Wood thrush: Hayes et al. 2020).~~,~~ These practical elements are invaluable to formulate effective conservation measures and facilitate population stability (Travis and Dytham 2013; Niebuhr et al. 2015, Endriss et al. 2019).

Understanding migratory decisions

In addition to using the Motus network to describe migration, it can facilitate an 'experimental' approach, i.e. extending laboratory-based studies in natural scenarios (Goymann et al. 2010 and Schmaljohann and Klinner (2020). For instance by radio-tagging "lean" and "fat" individuals of a species on a single day to minimize the effect of weather variation on the birds' departure decision (e.g. Karwinkel et al 2022, 2024). When numerous individuals subject to the same external conditions are tracked at the same time, this may then allow estimation of conditions when most individuals migrate (Delingat et al. 2008, Schmaljohann & Klinner 2020), for example during favourable winds (Lagerveld et al. *In Press)*.

Parameters derived from flights of individuals tracked with Motus such as departure and landing decisions, speed and routes (Figure 5a; Brust et al. 2019, Packmor et al. ~~2022~~2020, Brunner et al. 2022; Linhart et al. 2023, Ruppel et al. 2023~~a,b~~), can allow comparisons in behaviour among individuals of different populations, and those that orient across and around barriers (Figure 5b; Schmaljohann & Naef-Daenzer 2011, Woodworth et al. 2015; Brust and Hüppop 2022). An improved understanding of migration behaviour, its limitations and flexibility among different species, can help us to better predict how species might adapt to changes around them and improve efforts towards their conservation (Sutherland 1998).

Obtaining individual responses to environmental stressors

Motus can also address identifiable conservation concerns, and detect responses to specific forms of anthropogenic or environmental disruption. Anthropogenic structures, such as offshore wind turbines, can attract migratory birds, potentially causing increased mortality through collision (Perrow 2019) or evoke avoidance behaviour leading to increased, delayed, fitness costs due to longer routes and higher energy expenditure (Schwemmer et al. 2023). Such impacts are still largely unquantified on migratory populations of birds (Marques et al. 2021).~~, but using~~One possibility is to use Motus in combination with acoustic monitoring (as in Lagerveld et al. 2023), whereby we can localise the interaction of tracked individuals with near- and offshore infrastructure, ~~through careful placement of receiving stations on substations and energy platforms~~and contextualise these known individuals amongst con- and allospecifics, detected by the acoustic recorders (Loring et al. 2019, Willmott et al. 2023).

Other anthropogenic disruptors are (agro-) chemicals such as neonicotinoids, which can impair the progress of migration in different taxa (Cabrera-Cruz et al. 2020). Eng *et al.* (2019) used Motus tracking to show responses to neonicotinoid ingestion by White-crowned sparrows (*Zonotrichia leucophrys*), whereby migrating birds on stopover are severely impaired in their ability to fuel, despite significantly increasing the length of stopover.

Further, artificial light at night (ALAN) has been shown to attract night-migratory birds to bright, often urban, areas (McLaren et al. 2018, Smith et al. 2021, Horton et al. 2023). These areas may act as potential ecological traps (i.e., inadequate stopover sites that might present higher risk of mortality; Van Doren et al. 2021). Similarly, anthropogenic electromagnetic radiation ~~(“~~(‘electrosmog~~”)~~ ‘) has been shown to disrupt the magnetic compass of night-migratory songbirds (Engels et al. 2014). As this was observed in the lab environments with caged birds, it poses the question whether ‘electrosmog’ is also a hazard for freely moving birds in the wild. Here we can ~~Therefore, the extent of the effects of these hazards on individuals in the wild poses a suitable set of questions~~ to which to apply Motus tracking, where directional and time to depart data can be collected by local and regional arrays of receivers positioned in and around areas of high urban density.

Combining Motus tracking with physical samples

Simultaneously collecting samples (e.g. feathers, saliva, blood or faeces) that tell us something about the physiological state of the animals, together with movement behaviour, can help us better understand how the physiology of an individual influences its migratory decisions. The high temporal resolution of tracking with Motus now allows us to link physiological indicators, especially those changing rapidly (e.g. hormones), much closer to their movement ~~behaviour~~ (e.g. Eikenaar et al 2020). This could for example include site quality, by correlating stopover duration and habitat use, as recorded by Motus, with body condition and immune function (Schmaljohann & Naef-Daenzer 2011, Hegemann et al. 2018, Brust et al. 2022). This would allow us to understand whether the sites provide the necessary functions for stopover required by migrants. If not, targeted conservation measures could be taken to restore the missing functions.

~~Based on g~~Genetic analyses in conjunction with recorded migratory behaviour (direction and routes, which are accessible with the high spatiotemporal accuracy of Motus), ~~population-specific differences~~ could indicate population-specific differences and possible significant regions in the genetic structure that are important for the genetic coding of migratory behaviour (Ruegg et al. 2014, Bossu et al. 2022, Sharma et al. 2023). Blood and faecal samples could be used to monitor the prevalence of pathogens that can be linked to body condition, population origin and subsequent migration decisions (ideally seasonal migration success; Neima et al. 2020, Morales et al. 2022). In the long term, standardised studies of migratory behaviour combined with sampling of tagged individuals could allow predictions of responses to global climate and habitat changes (Saura et al. 2014, Anderson et al. 2019).

Practical next steps: the logistics of developing Motus for flyway level research

~~Currently, much of the European continent is not covered by Motus (Figure 4).~~ Achieving greater geographical, i.e. near-continental, coverage of the Motus network stations is underway. ~~, but~~ However, ~~to increase coverage, it will~~this requires a strategic placement plan, cf. Lefevre and Smith (2020), based around the key questions discussed in this essay, and the special physical features of European landscapes (Figures 4, 5). The ~~realisation~~ network will require significant capital investment and a collaborative spirit amongst researchers, conservationists and volunteers alike, because this task is too big for single groups.

Single groups ~~could~~ can realize regional-scale networks through discrete projects, which is a necessary way of completing a continent-wide network (Taylor et al. 2017, Griffin et al. 2020). Ideally, such projects fill in geographical gaps based on species ecology and migratory behaviour already garnered from other technologies (e.g. geolocators; Bayly et al. 2018, or radar; Robinson 2023). As well as capital, the development of the network will require significant time and focus to maintain equipment and retrieve data, particularly in remote areas. Such ~~remote~~ receivers are less likely to be monitored remotely because of signal and power restrictions, and therefore greater logistical efforts are required to obtain the stored data and undertake maintenance.

Cost per receiver can be realised for as little as €3000 - 5000 (~ four directional antennas, Sensorgnome receiver), but may approach €10000 dependent on requirements for installation and precise configuration of antennas. Each tag, whether from CTT or Lotek, is approximately €200, although this approaches €300 for the very smallest models. While cheaper than large, satellite enabled tags, this does not approach the low cost of metal or colour rings that allow researchers to capture and mark many ~~hundreds~~ thousands of birds. Cost reduction is hampered by limited market competition and a lack of open-source development, which contrasts the collaborative nature of Motus entirely, and must be addressed going forward to allow tagging on a much larger scale.

Lastly, the amount of data collected from Motus is enormous and is likely to continue to grow alongside other biologging data (López-López 2016), so appropriate statistical tools will need to continue to be develo~~p~~ped~~-~~. Complex Bayesian modelling frameworks to appropriately analyse Motus data have been developed, and tested in limited circumstances, e.g., modelling movement offshore (Cranmer et al. 2017; Baldwin et al. 2018), and estimating flight heights (Lagerveld et al. *In press*). Extending the applicability of these methods and developing integrated frameworks with multiple data types would enable researchers to make better use and further inferences about migratory parameters that can inform conservation (Gregory et al. 2023).

These challenges can only be solved in the long term, with a coordinated, international, collaborative effort. Platforms are needed to bring together multiple research groups to develop joint funding applications and to work together for the benefit of the wider Motus community. This community must contain academics, policymakers, government officials, ~~and~~ conservationists, amateur biologists and ecologists, ~~even amateur radio enthusiasts,~~ who can develop well-defined, focused study objectives. The involvement of a diverse number of stakeholders is required, not just to share the cost burden and coordination responsibilities, but also to ensure fair data sharing, and the direct integration of such data into policy and conservation actions (UNEP 2020, Gregory et al. 2023; Guilherme et al. 2023).

Final Outlook

In this time of rapid ecosystem disruption, it is vital to work collaboratively to conserve migratory species. We need to work at multiple scales to answer questions about how species are confronting environmental changes. Motus can provide multi-scale data on the movements of bird without the need for recapture, even on species as small as Nathusius pipistrelles *Pipistrellus nathusii* (Bach et al. 2022, Briggs et al. 2023, Lagerveld *et al. In Press*), Yellow-browed warbler *Phylloscopus inornatus*), and large insects, such as the monarch butterfly (Knight et al. 2019, Wilcox et al. 2021). Motus' features and capabilities make it an attractive and exciting prospect for exploring as yet unanswered ecological, evolutionary, and behavioural questions.

There is a significant amount of logistical and planning work to develop and grow the network to reach its full potential in terms of basic and applied science, but ~~effort to grow the network~~ such efforts ~~,~~that also focus on expanding the collaboration between ~~the involved~~ parties, and ~~realize~~ realizing developed conservation strategies will result in benefits for birds, nature as a whole and ultimately, by supporting the One Health approach, us as humans.

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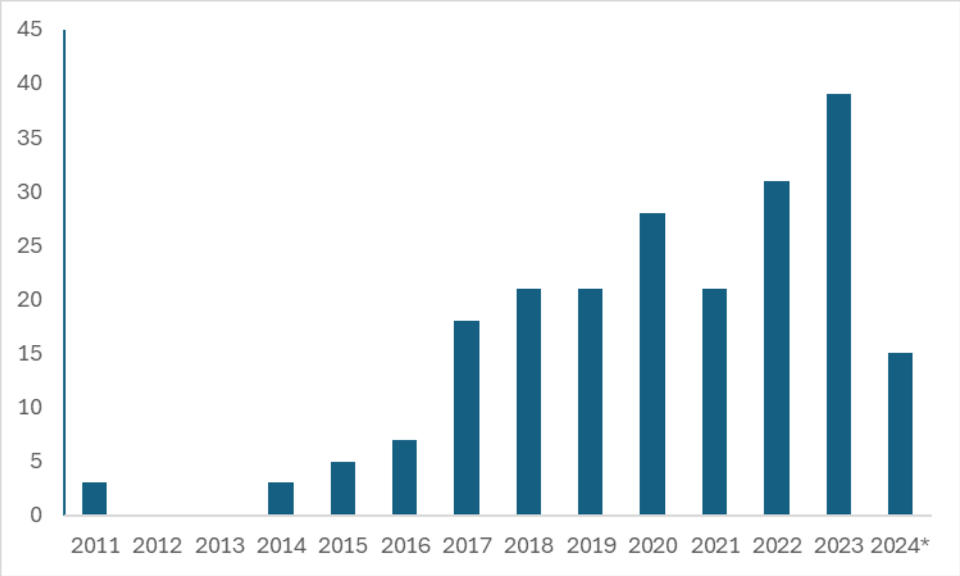


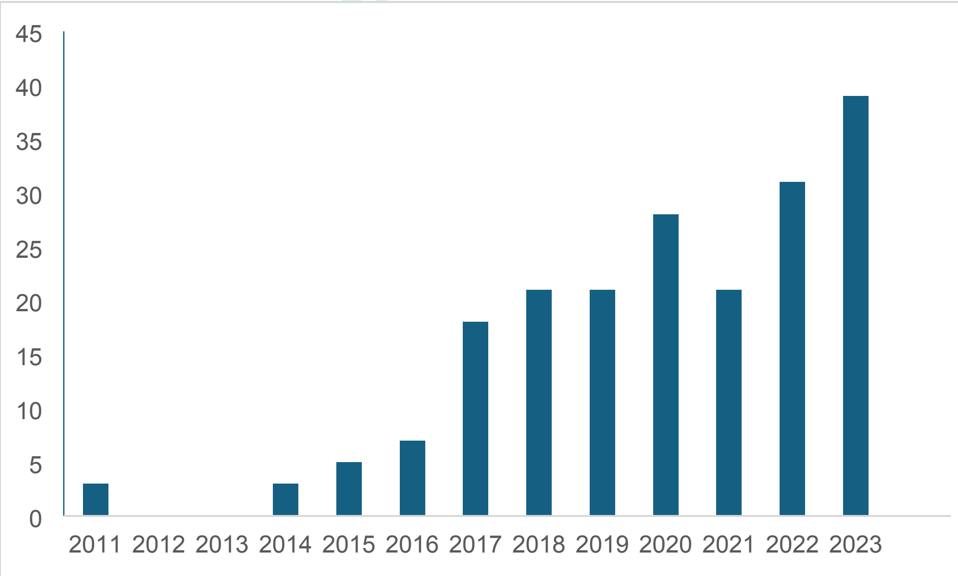


Figure 1: Number of publications per year (2011 – 2023), resulting from Motus data. * = to October 2024. Source: motus.org

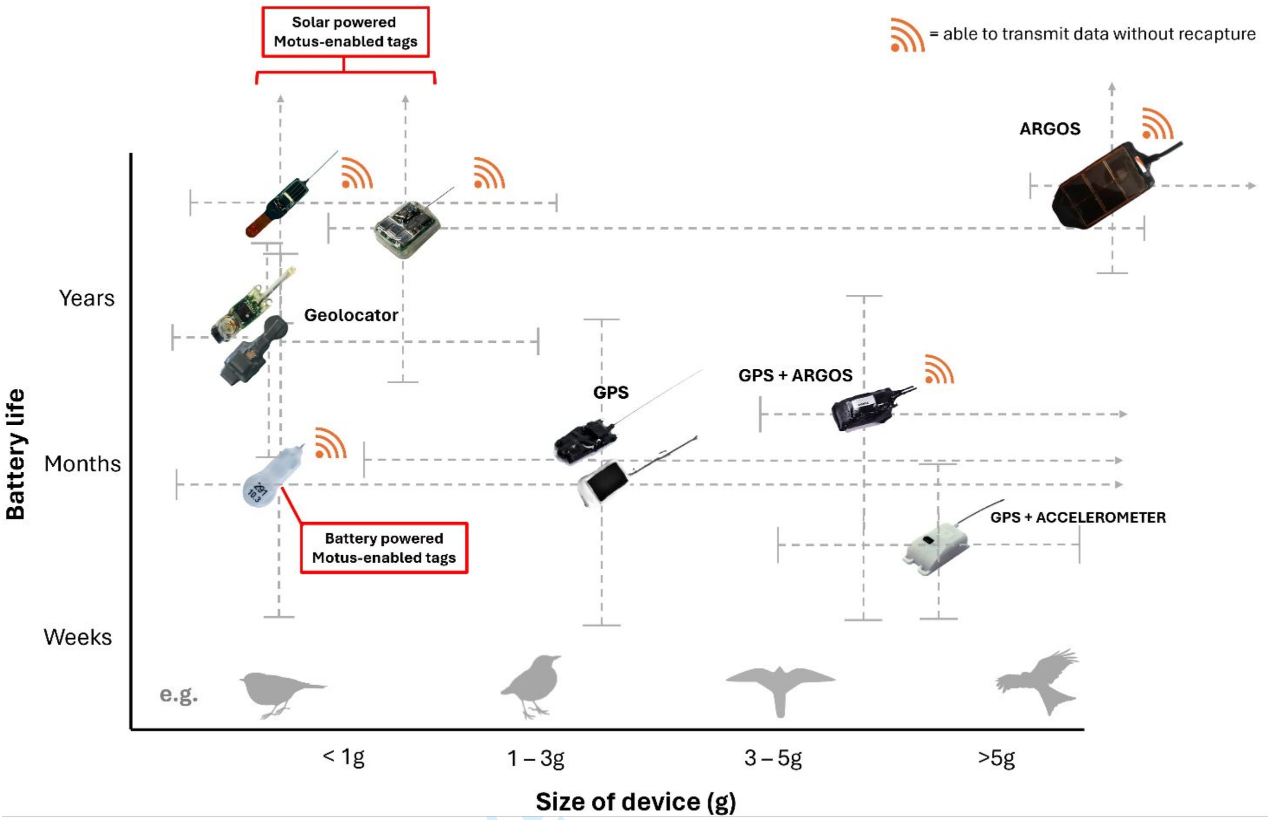


Figure 2: Capability and context of tags enabled for Motus. Icons indicate tag types and are positioned approximately in relation to their mean battery lifetime and size. Grey dotted lines represent variation on both axes taking into account programming influence on battery life and differences among and between device types. Orange 'wifi' symbols represent transmission capability, independent of the bird´s return to a specific location.

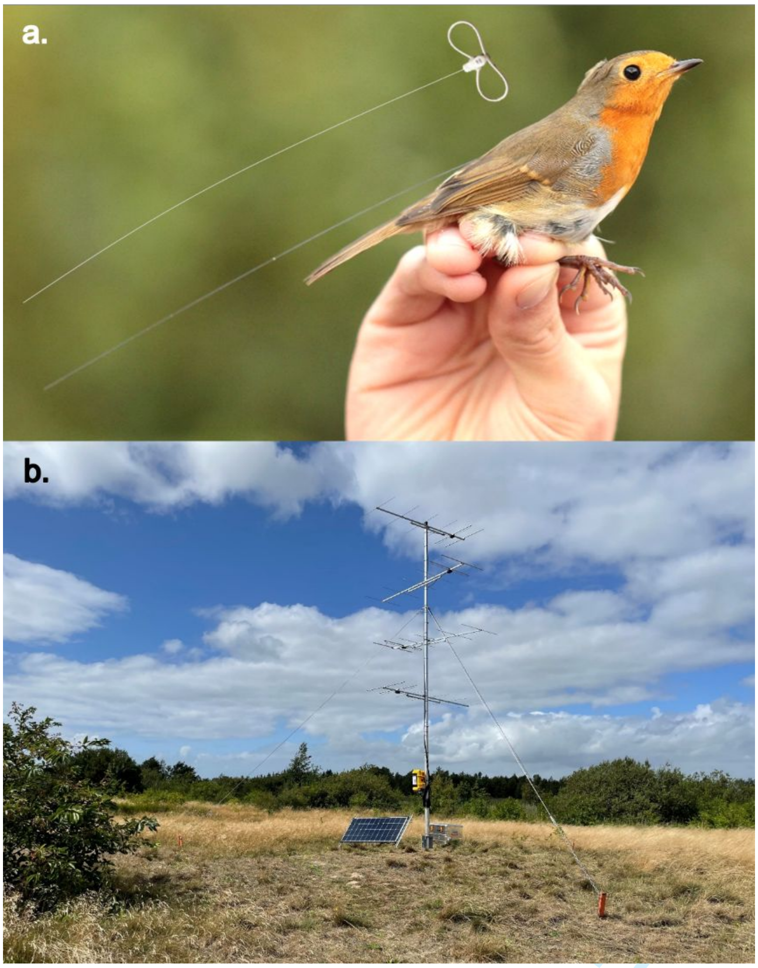
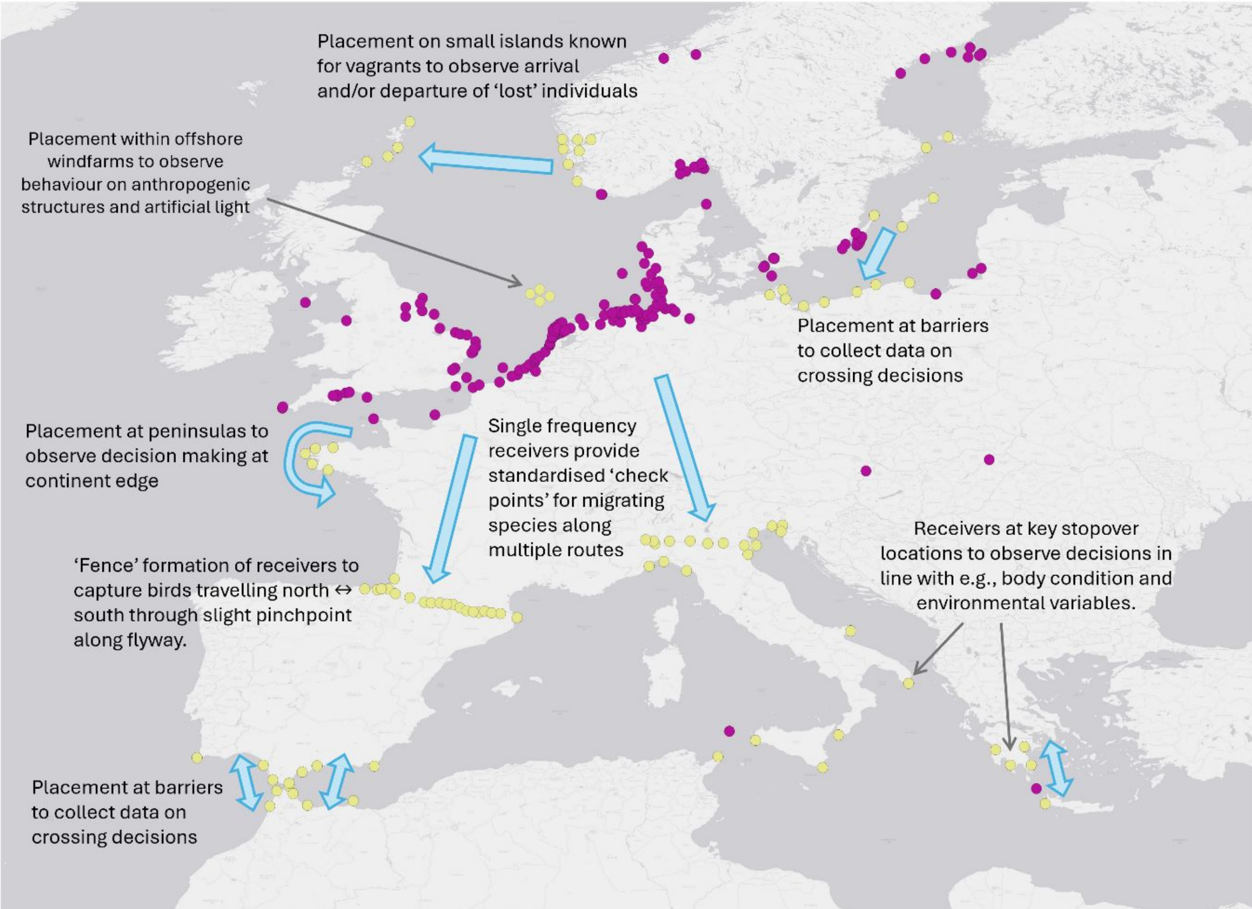


Figure 3a. European Robin (*Erithacus rubecula*) with attached radio transmitter with radio transmitter and attached leg-loop harness illustratively shown above the bird; b. a Motus receiving station (6 metre height), with 4 six-element-Yagi antennas pointing in four directions. The station is powered by solar, with a buffer battery (in aluminium box on ground). The electronics are installed in the small yellow box at the pole. Detailed information about tagging animals and building stations can be found at the Motus Webpage (motus.org/resources/) and from the regional Motus coordinators (motus.org/groups/regional-coordination-groups/). Photos: T.K.

922 

923 Figure 4: Current Motus receiving station network (purple dots) across the European
924 continent, along with hypothetical future stations (yellow dots) to demonstrate potential to answer
925 demographic and conservation-focused questions about bird migration. Blue arrows highlight flyways
926 and movements of particular study interest.

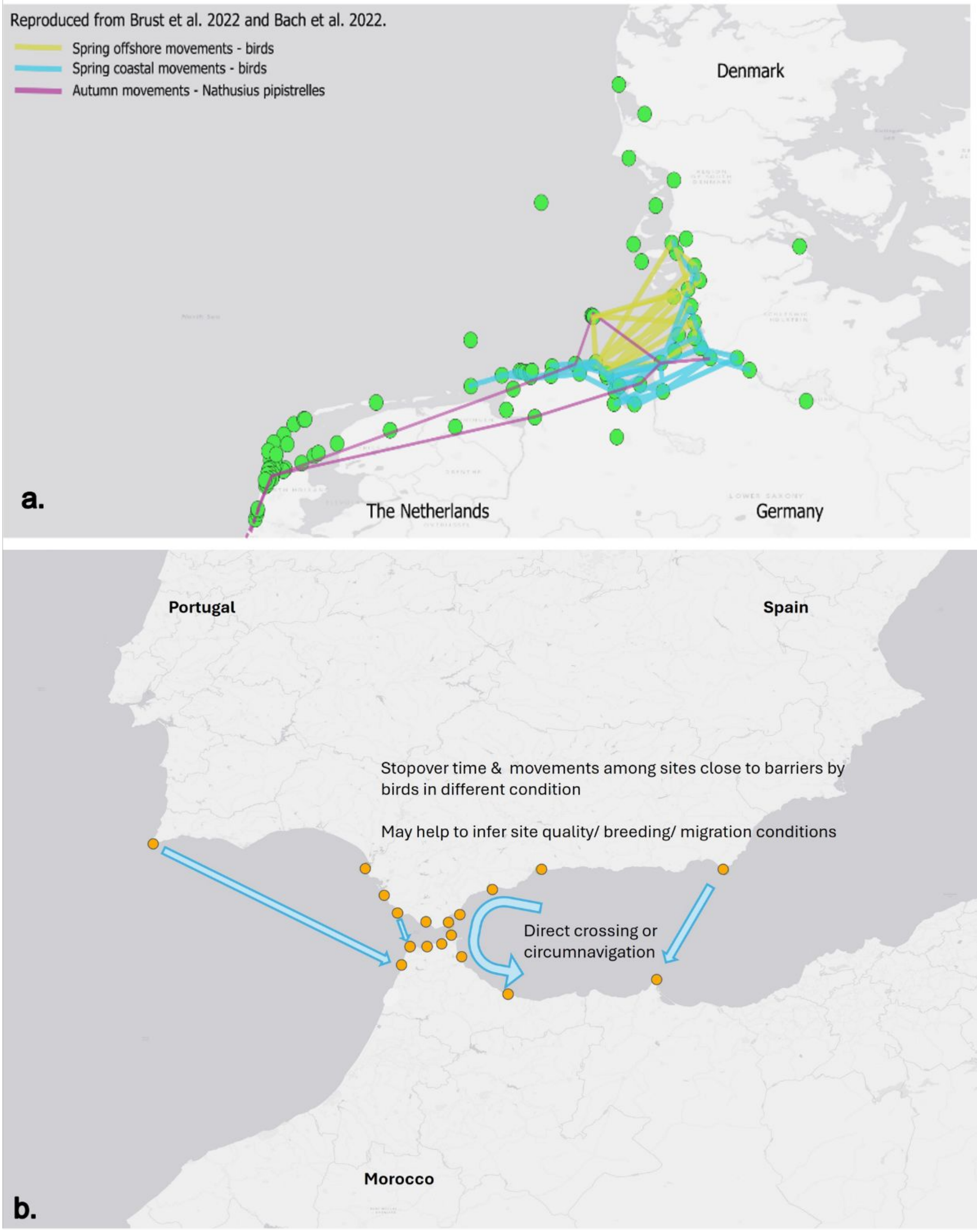


Figure 5: Studying behaviour of migrating animals at barriers; a: currently operational receiving stations (green dots) along the North Sea coast, and examples of tracks collected from birds and bats; b: examples of potential station placement (yellow dots) and data collection at Gibraltar, Iberian peninsula, where many thousands of migratory species will cross an important migratory barrier, the Mediterranean Sea. Blue arrows exemplify expected flight paths that could be detected by the set-up.