1 Scanning the skies for migrants: Conservation-focused

### 2 opportunities for a pan-European automated telemetry network

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29 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.

37 To mitigate their decline, research at a continental and flyway scale is required to adequately monitor changes in the demographic processes of 38 39 populations and understand the needs of migratory species, during all parts of the annual cycle. The Motus Wildlife Tracking System (Motus) could provide a solution 40 41 to data gaps that exist particularly for small and migratory species. Motus is an 42 automated telemetry system for animal tracking, which originated in North America. It provides a collaborative network by using the same VHF radio frequency for all 43 44 tracked individuals, in combination with an individual tag identifier. Motus can provide 45 information on movements made by individuals of the smallest bird and bat, and even larger insect species, thus aiding our understanding of aspects of their 46 47 migration that could impact demographic parameters.

Here we emphasise conservation-focused research opportunities, with a particular lense on European migrant taxa. We highlight examples from the existing network, and identify geographical gaps in the network which need to be filled to 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

- 53 drive to expand the network will improve its ability to conservation plans for such
- 54 species.

56 Introduction

Biodiversity loss driven by land use change, exploitation of natural resources, 57 and affected further by climatic disruption, is a defining feature of the Anthropocene 58 (Sala et al. 2000). A decline in habitat availability and significant disruption to 59 ecosystem structure, reducing critical services such as biomass production, 60 61 pollination and pest control, has led to declines in a wide range of taxa globally 62 (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 63 64 zoonotic and vector-borne diseases (Jaurequiberry et al. 2022), and pest outbreaks. These impacts affect species' distributions, abundances, fitness, and consequently 65 their ability to complete their life cycle successfully (Bellard et al. 2012). 66

67 Of particular concern are migratory species, which serve as ecological indicators and direct providers of vital contributions to ecosystem functioning, 68 including biomass production, pollination, pest control (Bauer and Hove 2014. 69 Satterfield et al. 2020). Migratory species experience a variety of environmental 70 conditions on their seasonal, sometimes trans-hemispheric journeys (Turbek et al. 71 72 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 73 74 requirements for reproduction and survival are no longer met (Birnie-Gauvin et al. 75 2020, Marcacci et al. 2022, Rigal et al. 2023). There are also additional threats such as hunting (Jiguet et al. 2019), augmentation of ecological barriers (Gauld et al. 76 77 2022), as well as increasingly unpredictable climatic patterns decoupling the phenology of ecologically linked species (Iler et al. 2021, Clarke et al. 2022). 78

79 Understanding the factors impacting the population status of migratory species, i.e., the changes in vital rates that drive population growth or decline, is 80 essential (Morrison et al. 2016). These species face challenges which directly 81 82 conflict with the multi-factorial optimisation of migration, which form often inherited, integrated migration strategies (Åkesson and Helm 2020; Schmaljohann et al. 2022, 83 Fattorini et al. 2023). Phenotypic flexibility and genetic change through heritable 84 85 traits ('micro-evolution') can facilitate some adjustments and adaptations (Hiemer et al. 2018, Ozsanlav-Harris et al. 2024). However, many migratory species cannot 86 87 respond to changes at a sufficiently rapid pace, meaning that population declines are widespread (Both et al. 2006, Wilcover & Wikelski 2008, Frick et al. 2017, 88 Rosenberg et al. 2019, Vickery et al. 2023). 89

90 The Convention on the Conservation of Migratory Species (CMS; Resolution 12.26) highlights the need for a multi-species, flyway level perspective in terms of 91 research into population declines (UNEP/CMS 2020, Frick et al. 2020, Marcacci et 92 al. 2022, Chowdury et al. 2023, Vickery et al. 2023). However, gathering sufficient 93 data from a robust number of individuals from different populations, is extremely 94 95 challenging (Morrison et al. 2016; McKinnon and Love 2018). Research at a flyway 96 scale is complicated and reliant on international collaboration (Nadal et al. 2020; 97 Vickery et al. 2023, Serratosa et al. 2024). This is particularly the case for our 98 smallest species, namely migratory passerines, waders and swifts, bats, and insects, 99 whose size and behaviour have rendered them difficult to study (Wikelski et al. 2007, Fiedler 2009, Bridge et al. 2013). Infact, we are only now beginning to properly 100 101 quantify the volumes of migratory insects crossing the continent (Hawkes et al. 102 2024), and the impact of this moving biomass is still little understood (Chapman et al. 103 2015).

104 Where are the knowledge gaps in the study of small migratory species?

105 Currently, we have little detailed spatial and temporal information on small bird, bat and insect migration. Broad scale migration patterns across Europe, 106 107 including concentrations of both avian and insect migrants passing through marine 108 and mountainous regions, have been identified using radar (Bruderer & Jenni 1990, 109 Bruderer & Liechti 1999, Nilsson et al. 2019, Weisshaupt et al. 2021, Hirschhofer et al. 2024). Yet radar data, derived from echo signatures, largely do not allow us to 110 111 tease out species-specific and indeed individual-level variation in large-scale movements (Schmaljohann et al. 2008, Zaugg et al. 2008), which would facilitate 112 113 links to demography, physiology and ecology.

In contrast, several million individuals have been marked using metal or 114 colour rings across Europe (Du Feu et al. 2016), contributing to our fundamental 115 116 ecological knowledge of bird movements. Yet recapture, recovery, or resighting 117 probability is often low (across 32 European level ringing schemes recovery rate for 118 all species combined varied from 0.6 - 7.6%; Baillie 1995), particularly on the 119 wintering grounds (only one of 49 Hoopoe Upupa epops and four of 121 Wryneck Jynx torguilla ringed in Europe and subsequently recovered, were found on the 120 121 African continent; Reichlin et al. 2009), and highly variable amongst species and 122 locations (Thorup et al. 2014).

Many of the disadvantages of the aforementioned methods can be addressed by tracking individuals and indeed, following their migratory movements. Flack and colleagues (2022) stress several major data-deficient migration research areas that could be filled by employing tracking, including how information on bird migration can be used to facilitate better conservation and management strategies. There are also

other fundamental biological processes that would benefit from individual tracking.
These include dispersal; more nomadic, non-breeding movements (Snell et al. 2018;
Mckinnon et al. 2019); as well as pre- and post-breeding movements (Mukhin et al.
2005, Züst et al. 2023).

However, individual tracking of small migrants requires tracking devices 132 133 weighing only 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, 134 135 McKinnon & Love 2018). Radio-tracking, however, has already reached masses of 136 under 0.5g, and the Motus Wildlife Tracking System (hereafter Motus, Taylor et al. 137 2017) is producing tags equivalent to, and lower than, the weight of the smallest geolocators. Here, with Motus as a methodological basis, we focus on conservation 138 139 and demographic-specific knowledge gaps in the study of small migratory birds, bats and insects. 140

#### 141 Motus – Automated VHF tracking technology

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). The initiation of Motus in Europe has been later and its growth slower, but there is now a dense network of stations along the coasts of Germany and the Netherlands, and to a lesser extent in Sweden, Denmark, Belgium and the UK, with a number of additional stations in other countries, and on offshore research and energy platforms.

Motus exploits a network of passive VHF receivers (Figure 2), aligned on the same frequency, which continuously receive and record uniquely-coded signals of tagged individuals, using directional Yagi antennae, without the need for recapture

(Mitchell et al. 2015; Taylor et al. 2017; Mckinnon et al. 2019; Imlay et al. 2020). The
lightest tags currently available weigh 0.13 g and have a maximum interval between
pulses of 29 s, which can provide 20-22 days of data. Researchers are able to select
from among a number of options and device parameters (burst interval, battery or
solar power, attachment and antenna type), in line with their specific question (Figure
1). With the Motus system, it is now possible to track movements of light insects,
such as the monarch butterfly (Knight et al. 2019, Wilcox et al. 2021).

159 Motus is already producing important insights into the movements of birds, bats, and insects. For example, Gómez et al. (2014) and Zenzal et al. (2021) 160 161 revealed the intricacies of strategies of birds crossing the Gulf of Mexico; and Brunner et al. (2022) discovered several unknown aspects of migratory connectivity 162 163 and ecology in the elusive Swainson's warbler Limnothlypis swainsonii. Studies in Europe are now beginning to understand more about the migratory and pre-164 165 migratory movements of Nathusius pipistrelles *Pipistrellus nathusii* (Bach et al. 2022, 166 Briggs et al. 2023) and sea-crossing of thrushes (Brust et al. 2019). The existing work suggests myriad areas for future studies that would benefit greatly from using 167 168 automated VHF telemetry. These examples show that Motus can be a tool to obtain 169 a 'holistic' view of species' ecology, by gathering data on groups and time periods 170 (e.g. juvenile fledging) previously understudied (Martell et al. 2023).

# How Motus can help to address knowledge gaps in migratory taxamovement

To understand population change and guide conservation measures, we need data on key population parameters, which necessarily require long-term, broad spatial scale, annual cycle data collection (Satterfield et al. 2020). Yet, funding, time,

176 and staff resources, and the vast areas over which migration occurs, make this difficult (Lefevre and Smith 2020). A relatively low-cost, collaborative, spatially 177 dispersed network of Motus stations can essentially create a vast open-air 178 179 laboratory. Taylor et al. (2017) presented a detailed account of the benefits and opportunities of Motus, as well as areas that require further development and 180 investment, but we address here the key strengths and challenges that we perceive 181 182 in relation to pertinent conservation focused questions and in the context of other tracking devices. 183

184 Firstly, receiving stations can be placed anywhere (see Figure 2b) and be controlled remotely, and this autonomy means that data capture efforts are less 185 limited by researcher effort, in contrast to commonly used methods such as bird 186 187 ringing (Griffin et al. 2020; Flack et al. 2022). Fixed positioning of the receiving 188 stations, along with a unrestricted recording period, also enables standardized data 189 collection and reduces observer-bias (Griffin et al. 2020). Secondly, there is no 190 requirement to recapture the birds to retrieve data, which can be recorded by one or 191 more stations. In this way, Motus reduces bias encountered in studies where all 192 information derives only from the fraction of successfully recaptured individuals (as 193 with data loggers). Another benefit is that tracking occurs in near real time, as long 194 as receivers are able to transfer data to the server quickly.

Lastly, 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). Pinpointing specific sites for targeted conservation efforts is important, given that limited, localised stopover site use could induce higher vulnerability in certain migrating species (Bayly et al. 2013; Gómez et

al. 2014). Motus' potential to help create species actions plans in this way has been
recognised outside of the research community, and recommendations for its use to
monitor understudied small species are included in the records from COP13 on the
Convention of Migratory Species (UNEP/CMS 2020). Widespread adoption of Motus
by conservation and research organisations, who may then allow others to install
Motus stations on their land, could vastly improve network coverage.

207 Still, there are some caveats. Most Motus studies do not report a 100% 208 detection rate; reporting rates are closer to 50-70% (Crewe et al. 2020), even when 209 the tags are deployed close to a receiving station. Potential reasons for this are: 210 habitat type and topography, weather conditions, characteristics of the antennae and the flight altitude and orientation of the animal in relation to the antennas of the 211 212 receiver (Crewe et al. 2020). Furthermore, the network of stations is still patchy and 213 this low spatial coverage does not yet allow continuous tracking across the continent 214 in Europe, and is particularly sparse where data are lacking the most in eastern 215 Europe. With this opinion paper, we hope to further spark the collaborative spirit of Motus to create a denser network in Europe and resemble the situation in North 216 217 America.

218 Obtaining demographic information using Motus

Understanding when and where differences in population processes occur, is notoriously difficult (Doerr and Doerr 2005; Border et al. 2017, Telensky et al. 2020). Migrating species are diverse in their timing, routes, distance and speed, but most employ repeated, alternating migratory and stationary periods for resting, recovering and fuelling (Alerstam et al. 2003; Åkesson and Hedenström 2007; Schmaljohann et al. 2022). Differences among species in the location and timing of these patterns

may affect how pressures accumulate and carry over, and therefore how strongly
their populations are impacted by interacting environmental changes (Sawyer *et al.*2009, Patchett *et al.* 2018, Nadal et al. 2022; Rueda-Uribe et al. 2022).

228 Quantifying variation in a number of different life history processes, primarily 229 survival, mortality, emigration/ immigration (dispersal), as well as immediate 230 behavioural responses to environmental stressors, can then direct conservation 231 efforts for these populations and/or species (Gómez et al. 2021, DeMars et al. 2023). 232 In the following sections, we address these different life history processes, identifying 233 the most profitable opportunities to expand our knowledge of small species 234 migration, using Motus.

#### 235 Survival and mortality

236 Survival and mortality clearly affect population dynamics, altering age and sex 237 structure (Schorcht et al. 2009), and affecting future reproduction (Saracco et al. 238 2008). Within migratory species, variation in survival among populations can be 239 linked to alternative routes and their different pressures (Hewson et al. 2016). Pressures can create pinch points, which may lower fitness and increase mortality 240 241 (Dhanjal-Adams et al. 2017), particularly those that support high numbers of 'comigrants' (multiple species moving through major sites and corridors simultaneously 242 243 - Cohen et al. 2021). The convergence of otherwise spatially segregated populations 244 at single locations may also have additional consequences for disease transmission (Cohen et al. 2021). 245

Focusing Motus station placement at key staging areas, bottlenecks and barriers, in closely-packed 'fence' or 'curtain' formation (Figure 3) would provide 'checkpoints' for tagged migrants, leading to the comparison of local apparent

survival rates along and among different routes for multiple populations of different
species, and under a range of environmental conditions. Because of the single
frequency strategy, 'hits' from different individuals of different species can be collated
with ease to denote flyway-level site importance. Stations on either side of barriers
could also provide insights into how migratory animals assess the scale of the barrier
in front of them (Figures 3, 4).

If there are sufficient stations along a route (and adequate numbers of tagged 255 256 individuals), then obstacles that slow down or terminate migration can be identified. 257 Parameters derived from flights of individuals tracked with Motus such as speed, routes (Brust et al. 2019, Brunner et al. 2022; Linhart et al. 2023), can allow 258 comparisons among individual birds, bats or insects of different populations, and 259 260 those that orient across and around barriers (Woodworth et al. 2015; Brust and 261 Hüppop 2022). Currently little is known about locations of high mortality across 262 Europe for small migrating taxa (acknowledged by Serratosa et al. 2024, specific 263 locational information and cause of death is limited to larger migratory species with accurate positional loggers). For migratory insects, incomplete trajectory information, 264 265 including locations of stopover sites and wintering areas hinders the implementation 266 of any conservation plans (Chowdury et al. 2021). This need should encourage us to place receiving stations at known - and suspected - locations of stopover and 267 268 potential mortality (e.g. Figure 4b).

#### 269 Dispersal, immigration and emigration

Juvenile and post-breeding dispersal are critical but understudied fundamental biological processes, consisting of the initial process of emigration from a breeding site, and the subsequent immigration to another the following season (Matthysen & Clobert 2012). Data are particularly needed from young individuals to

assess when juveniles make decisions about breeding site settlement (Doerr and
Doerr 2005; Mukhin et al. 2018). For species with discrete breeding sites restricted
by habitat, some populations may display genetic structure that could increase and
become inbred with further habitat loss and climate change (Day et al., 2023).
Understanding how these populations are connected through immigration and
emigration is important for deciding what conservation measures might be useful
(Driscoll et al. 2014).

281 We can derive differential rates of emigration and immigration of a species of 282 interest, among different locations (le Roux and Nocera 2021) through 283 comprehensive tagging campaigns (ethical considerations of such projects notwithstanding – Soulsbury et al. 2020), supported by groups of Motus stations 284 285 around key breeding sites. Using Motus, juvenile Blackpoll warblers (Setophaga striata), Kirtland's Warbler (Setophaga kirtlandii) and Barn Swallow (Hirundo rustica), 286 287 have been shown to make large exploratory movements upon fledging prior to 288 migration (Brown and Taylor 2015, 2017; Evans 2018; Cooper and Marra 2020). Questions remain about the function of such exploratory movements (Züst et al. 289 290 2023), in particular because long-distance dispersal to new breeding sites appears to 291 be rare overall, although potentially underestimated given the difficulty of monitoring 292 such movements. It is unclear how this exploration may relate to range expansion 293 and individual or species responses to climate change (Driscoll et al. 2014).

Motus can facilitate local to large scale, low effort tracking, and its ability to expand spatially and temporally beyond the capabilities of manual VHF tracking can increase the power of both juvenile fledging studies (Cox et al. 2012), and mediumlong distance post-breeding dispersal (Evans et al. 2018, Hayes et al. 2024). Practical conservation decisions could benefit from understanding how far and in

what direction juveniles disperse, and how individual phenotypes and condition
levels (Morales et al. 2010) might lead to differential survival based on fledging
strategy (Evans et al. 2020) and surrounding habitat quality (Hayes et al. 2020).
Knowledge of this variation within and among species, gained by observing dispersal
movements using Motus, could drive conservation measures that would facilitate
population stability (Travis and Dytham 2013; Niebuhr et al. 2015, Endriss et al.
2019).

#### 306 Identification of Stopover sites

307 We can identify the importance of stopover sites with strategic placement of Motus stations. Smetzer and King (2018) used a regional Motus network at the Gulf 308 of Maine of the United States, and identified the use of a major staging area for 309 Blackpoll warblers (Setophaga striata) and Red-eyed Vireos (Vireo olivaceous). The 310 311 directional information collected by Motus showed that tagged individuals originated 312 from multiple breeding populations across the North American continent, 313 demonstrating the area's importance to the two species nationally. Such a study could be carried out at similar areas in Europe such as in the large natural wetlands 314 315 in the Bay of Biscay, and the Strait of Gibraltar (Figure 4b), and therefore could be 316 used to focus conservation resources.

#### 317 <u>Understanding migratory decisions</u>

Motus can facilitate a 'quasi-experimental' approach as proffered and demonstrated by Goymann et al. (2010) and Schmaljohann and Klinner (2020), and can extend capture-mark-recapture studies such as that undertaken by Knoblauch et al. (2021) and Menz et al. (2022), on dragonflies and moths respectively. Studies on insects have shown reliance on both celestial and sun compasses, as with birds

(Åkesson et al. 1996), and that there is significant selection of favourable winds, to
facilitate their journeys over and around barriers (Menz et al. 2022).

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), as well as better understanding of 'optimal' strategies (Åkesson et al. 2002, Hedenström 2008). Such fundamental understanding of migration processes can also help to prioritise important locations to target for conservation or management.

#### 331 Exploring the evolution of migratory routes via vagrants

Motus could also play a role in improving our understanding of vagrants, for 332 333 example how they act as potential agents of evolution of new migratory routes and/or 334 of range expansion (Dufour et al. 2022). Their influence on population change has only been explored in a few cases, for example that of Richard's Pipit (Dufour et al. 335 336 2023). For example, small songbirds, travelling in a westerly direction from Siberian 337 breeding grounds, and are hard to track because of their small size and distant, widespread, less accessible breeding grounds (Dufour et al. 2021). Such knowledge 338 339 gaps could be addressed using Motus by detecting departure directions of vagrants. 340 Motus can collect data on unsuccessful phenotypes, i.e. individuals that would not be recaptured anyway. Studies could investigate the fate of vagrants in the north-341 342 western parts of Europe (e.g., the UK and Republic of Ireland, Helgoland; Thorup et al. 2012), and a potential candidate for this research might be the Yellow-browed 343 344 warbler (*Phylloscopus inornatus*), as suggested by Dufour et al. (2022).

#### 345 Obtaining individual responses to environmental stressors

Motus studies of individuals can also address identifiable conservation 346 concerns, and detect how animals respond to specific forms of anthropogenic or 347 348 environmental disruption. Obstructions, such as wind turbines, can incur extra fitness pressure from detours, as well as direct mortality. Impacts are still largely 349 350 unquantified on migratory populations of birds (Margues et al. 2021) and bats (Lagerveld et al. 2014, Bach et al. 2022, although see Serratosa et al. 2024). Motus 351 has been used to track Nathusius pipistrelles (Pipistrellus nathusii) migrating along 352 353 the coast and to islands (Bach et al. 2022). Using Motus in combination with acoustic 354 monitoring (Lagerveld et al. 2023), we can localise the interaction of individuals with 355 near- and offshore infrastructure, through careful placement of receiving stations on substations and energy platforms (Loring et al. 2019, Willmott et al. 2023). 356

Other anthropogenic disruptors are (agro-) chemicals such as neonicotinoids, 357 358 which can impair the progress of migration (Cabrera-Cruz et al. 2020). Eng et al. 359 (2019) used Motus tracking to show responses to neonicotinoid ingestion by Whitecrowned sparrows (Zonotrichia leucophrys), whereby migrating birds on stopover are 360 361 severely impaired in their ability to put on fat, vital for migration, despite significantly increasing the length of stopover. In contrast, Wilcox et al. (2021) found no 362 impairment of Monarch butterflies Danaus Plexippus when tracked with Motus, after 363 being given the neonicotinoid Clothianidin. 364

Further, artificial light at night (ALAN) poses a potential thread for migratory birds (McLaren et al. 2018, Smith et al. 2021). From large-scale radar analyses we know that night-migratory birds are attracted to bright areas (Horton et al. 2023), where birds can be drawn into potential ecological traps (i.e., inadequate stopover sites that might present higher risk of mortality; disorientation; Van Doren et al.

370 2021). However, the extent of this effect on individuals has not been examined, yet, 371 which poses a suitable question to apply Motus tracking. Similarly, anthropogenic electromagnetic radiation ("electrosmog") has been shown to disrupt the magnetic 372 373 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 374 also a hazard for freely moving birds in the wild. Once properly understood, 375 376 appropriate mitigation and conservation can be designed and further tested to reduce the environmental impact of humans on migratory animals in the future. 377

#### 378 Combining Motus tracking with physical samples

Motus movement data can be collected alongside physical samples (e.g., 379 380 feathers, morphological measurements, blood and faeces). Such samples can help 381 us understand links between physical condition and site quality, for example by 382 measuring stopover time, habitat use, direction of departure, and correlating with 383 immune function (Schmaljohann & Naef-Daenzer 2011, Hegemann et al. 2018, Brust 384 et al. 2022). Additional genetics could be particularly valuable if information on putative origin of individuals could also be inferred (Ruegg et al. 2014), thus 385 386 shedding light on the genetic architecture underlying migratory patterns in different 387 populations (Bossu et al. 2022, Sharma et al 2023). Blood and faecal samples could be used to monitor pathogen prevalence, which can be linked to physical condition, 388 population origin, and subsequent movement decisions (Taylor et al. 2011, Neima et 389 390 al. 2020), all of which may give insights into population declines and predict 391 responses to global climate and habitat change (Saura et al. 2014, Anderson et al. 2019). 392

Practical next steps: the logistics of developing Motus for flyway levelresearch

Currently, there are vast areas across the European continent that are not yet 395 covered by Motus, but the collaboration of researchers in North America has 396 397 demonstrated that it is possible to obtain a near-continent-wide network of Motus stations. One major challenge European researchers encounter is the lack of a 398 399 single frequency the tags emit the signal. Whilst in a number of European countries 400 the frequency of 150.1 MHz is authorised either temporarily or permanently for wild animal telemetry tracking, in others only an alternative frequency is permitted. 401 Although multi-frequency detection by Motus receivers is possible, for example 402 403 introducing the licence-free frequency 434 MHz alongside the commonly used 150.1 MHz frequency in Europe, it incurs additional expense for extra equipment. 404

405 A second challenge is achieving sufficient spatial coverage by Motus stations. The progress of a continent-wide network comprised of potentially hundreds of 406 different stakeholders across many nations is a big task and will require a strategic 407 408 placement plan (Lefevre and Smith 2020), concentrating on coastlines, barriers or bottlenecks (Figures 3, 4). A complementary focus on regional-scale networks, which 409 410 can feasibly be funded as part of a discrete project, is also necessary, essentially 411 forming a dual bottom-up/ top-down approach (Taylor et al. 2017, Griffin et al. 2020). Regional projects could be structured in such a way that they 'fill in' gaps while 412 413 meeting study-specific design features. Key clusters of stations could be efficiently 414 positioned according to detection likelihood, but focusing on areas where we have 415 little information collated (Griffin et al. 2020).

416 Lastly, the amount of data harvested from Motus is huge and will likely continue to grow alongside other biologging data (López-López 2016) and will 417 require the continued development of appropriate statistical tools. Complex Bayesian 418 419 modelling frameworks to appropriately analyse Motus data have been developed, and have been tested in limited circumstances, e.g., modelling movement offshore 420 421 related to avian wind turbine interactions (Cranmer et al. 2017; Baldwin et al. 2018). 422 Extending the applicability of these methods and developing integrated frameworks with multiple data types would enable researchers to make better use and further 423 424 inferences about migratory parameters that can inform conservation (Gregory et al. 2023). 425

These challenges can only be solved in the long term, with a coordinated, 426 427 international, collaborative effort. Platforms are needed to bring together multiple research groups to develop joint funding applications and to work together for the 428 429 benefit of the wider Motus community. This community must contain academics, policymakers, government officials, and conservationists, who can develop well-430 defined, focused study objectives. The involvement of a diverse number of 431 432 stakeholders, not just to share the cost burden and coordination responsibilities, but 433 also to ensure fair data sharing, and the direct integration of such data into policy 434 and conservation actions (UNEP 2020, Gregory et al. 2023; Guilherme et al. 2023).

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437 Final Outlook

In this time of transformation and ecosystem disruption globally, it is vital to 438 work collaboratively to conserve migratory species efficiently. We need to work at the 439 right scale to answer questions about how species are confronting environmental 440 changes. Motus can provide data at a local, regional and intercontinental scale, on 441 442 the movements of our smallest bird, bat, and even some insect species, without the 443 need for recapture. With such data we can address conservation-relevant questions 444 to fill the corresponding gaps in knowledge so that effective conservation measures 445 can be more precisely formulated for the species in focus. Motus' features and capabilities make it an attractive and exciting prospect for exploring as yet 446 447 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, expand the collaboration between the involved parties and realize the thereout developed conservation strategies will result in benefits for birds, nature as a whole and ultimately, us as humans.

453

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#### 475 <u>References</u>

Åkesson, S., Alerstam, T., & Hedenström, A. (1996). Flight initiation of nocturnal passerine migrants
in relation to celestial orientation conditions at twilight. Journal of Avian Biology, 95-102.

478 Åkesson, S., Walinder, G., Karlsson, L., & Ehnbom, S. (2002). Nocturnal migratory flight initiation in

- 479 reed warblers Acrocephalus scirpaceus: effect of wind on orientation and timing of
- 480 migration. Journal of Avian Biology, 33(4), 349-357.
- Åkesson, S. and Hedenström, A., 2007. How migrants get there: migratory performance and
  orientation. BioScience, 57(2), pp.123-133.
- 483 Åkesson S, Helm B (2020) Endogenous Programs and Flexibility in Bird Migration. Front Ecol Evol

- 484 8:1–20. https://doi.org/10.3389/fevo.2020.00078
- Åkesson S, Ilieva M, Karagicheva J, et al (2017) Timing avian long-distance migration: From internal
  clock mechanisms to global flights. Philos Trans R Soc B Biol Sci 372:.
- 487 https://doi.org/10.1098/rstb.2016.0252
- Alerstam, T., Hedenström, A. and Åkesson, S., 2003. Long-distance migration: evolution and
  determinants. *Oikos*, *103*(2), pp.247-260.
- 490 Anderson AM, Duijns S, Smith PA, et al (2019) Migration Distance and Body Condition Influence
- 491 Shorebird Migration Strategies and Stopover Decisions During Southbound Migration. Front
- 492 Ecol Evol 7:1–14. https://doi.org/10.3389/fevo.2019.00251
- 493 Bach, P., Voigt, C.C., Göttsche, M., Bach, L., Brust, V., Hill, R., Hüppop, O., Lagerveld, S.,
- 494 Schmaljohann, H. and Seebens-Hoyer, A., 2022. Offshore and coastline migration of radio-
- 495 tagged Nathusius' pipistrelles. *Conservation Science and Practice*, 4(10), p.e12783.
- Baillie, S.R., 1995. Uses of ringing data for the conservation and management of bird populations: a
  ringing scheme perspective. Journal of Applied Statistics, 22(5-6), pp.967-988.
- 498 Baldwin JW, Leap K, Finn JT, Smetzer JR (2018) Bayesian state-space models reveal unobserved
- 499 off-shore nocturnal migration from Motus data. Ecol Modell 386:38–46.
- 500 https://doi.org/10.1016/j.ecolmodel.2018.08.006
- 501 Barron, D. G., Brawn, J. D., & Weatherheard, P. J. (2010). Meta-analysis of transmitter effects on
- avian behaviour and ecology. Methods in Ecology and Evolution, 1, 180–187.
- 503 https://doi.org/10.1111/j.2041-210X.2010.00013.x
- Bauer, S. and Hoye, B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning
  worldwide. Science, 344(6179), p.1242552.
- Bauer S, Shamoun-Baranes J, Nilsson C, et al (2019) The grand challenges of migration ecology that
   radar aeroecology can help answer. Ecography (Cop) 42:861–875.
- 508 https://doi.org/10.1111/ecog.04083
- 509 Bayly NJ, Gómez C, Hobson KA (2013) Energy reserves stored by migrating Gray-cheeked Thrushes
- 510 Catharus minimus at a spring stopover site in northern Colombia are sufficient for a long-

- 511 distance flight to North America. Ibis (Lond 1859) 155:271–283. https://doi.org/10.1111/ibi.12029
- 512 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. and Courchamp, F., 2012. Impacts of climate
  513 change on the future of biodiversity. Ecology letters, 15(4), pp.365-377.
- 514 Birnie-Gauvin K, Lennox RJ, Guglielmo CG, et al (2020) The Value of Experimental Approaches in
- 515 Migration Biology. Physiol Biochem Zool 93:210–226. https://doi.org/10.1086/708455
- 516 Border JA, Henderson IG, Ash D, Hartley IR (2017) Characterising demographic contributions to
- 517 observed population change in a declining migrant bird. J Avian Biol 48:1139–1149.
- 518 https://doi.org/10.1111/jav.01305
- 519 Bossu CM, Heath JA, Kaltenecker GS, et al (2022) Clock-linked genes underlie seasonal migratory
- 520 timing in a diurnal raptor. Proc R Soc B Biol Sci 289:. https://doi.org/10.1098/rspb.2021.2507
- 521 Both, C., Bouwhuis, S., Lessells, C.M. and Visser, M.E., 2006. Climate change and population
- 522 declines in a long-distance migratory bird. *Nature*, *441*(7089), pp.81-83.
- Bridge, E., Thorup, K., Bowlin, M., Chilson, P., Diehl, R., Fléron, R., Hartl, P., Kays, R., Kelly, J.,
  Robinson, W. and Wikelski, M. 2011. Technology on the move: Recent and fourthcoming
  innovaions for tracking migratory birds. Bio Sci, 61: 689-698
- 526 Briggs, P., Briggs, B., Parsons, E. A. 2023. First Motus tag results from BEdfont Lakes study of
  527 Nathusius' pipistrelle, British Island Bats 4, 46 60.
- 528 Brown, J.M. and Taylor, P.D., 2015. Adult and hatch-year blackpoll warblers exhibit radically different
- 529 regional-scale movements during post-fledging dispersal. *Biology Letters*, *11*(12), p.20150593.
- 530 Brown JM, Taylor PD (2017) Migratory blackpoll warblers (Setophaga striata) make regional-
- 531 scale movements that are not oriented toward their migratory goal during fall. Mov Ecol 5:1–13.
- 532 https://doi.org/10.1186/s40462-017-0106-0
- 533 Bruderer, B., and L. Jenni. 1990. Migration across the Alps. Pages 61–77 in Bird Migration:
- 534 Physiology and Ecophysiology (E. Gwinner, Ed.). Springer Verlag, Berlin.
- Bruderer & Liechti (1999) Bird migration across the Mediterranean. In Adams, N. & Slotow, R. (eds)
  Proc. Int. Ornithol. Congr., Durban: 1983-1999, Johannesburg: BirdLife South Africa.
- 537 Brunner AR, Dossman BC, Jirinec V, et al (2022) Migratory behavior and connectivity revealed in a

- 538 secretive Neotropical migratory songbird, the Swainson's Warbler. J F Ornithol 93:.
- 539 https://doi.org/10.5751/jfo-00134-930305
- 540 Brust, V., Michalik, B. and Hüppop, O., 2019. To cross or not to cross-thrushes at the German North
- 541 Sea coast adapt flight and routing to wind conditions in autumn. Movement ecology, 7, pp.1-10.
- 542 Brust V, Eikenaar C, Packmor F, et al (2022) Do departure and flight route decisions correlate with
- 543 immune parameters in migratory songbirds? Funct Ecol 36:3007–3021.
- 544 https://doi.org/10.1111/1365-2435.14187
- 545 Brust V, Hüppop O (2022) Underestimated scale of songbird offshore migration across the south-
- 546 eastern North Sea during autumn. J Ornithol 163:51–60. https://doi.org/10.1007/s10336-021547 01934-5
- 548 Cabrera-Cruz SA, Cohen EB, Smolinsky JA, Buler JJ (2020) Artificial light at night is related to broad-
- 549 scale stopover distributions of nocturnally migrating landbirds along the Yucatan Peninsula,
- 550 Mexico. Remote Sens 12:1–32. https://doi.org/10.3390/rs12030395
- 551 Chowdhury, S., Jennions, M.D., Zalucki, M.P., Maron, M., Watson, J.E. and Fuller, R.A., 2023.
- 552 Protected areas and the future of insect conservation. Trends in Ecology & Evolution, 38(1),553 pp.85-95.
- Clarke, B., Otto, F., Stuart-Smith, R. and Harrington, L., 2022. Extreme weather impacts of climate
   change: an attribution perspective. Environmental Research: Climate, 1(1), p.012001.
- 556 Cohen, E.B. and Satterfield, D.A., 2020. 'Chancing on a spectacle:'co-occurring animal migrations
  557 and interspecific interactions. *Ecography*, *43*(11), pp.1657-1671.
- 558 Cohen EB, Horton KG, Marra PP, et al (2021) A place to land: spatiotemporal drivers of stopover
- habitat use by migrating birds. Ecol Lett 24:38–49. https://doi.org/10.1111/ele.13618
- 560 Cooke, S.J., Piczak, M.L., Singh, N.J., Åkesson, S., Ford, A.T., Chowdhury, S., Mitchell, G.W., Norris,
- D.R., Hardesty-Moore, M., McCauley, D. and Hammerschlag, N., 2024. Animal migration in the
   Anthropocene: threats and mitigation options. *Biological Reviews*.
- 563 Cooper NW, Marra PP (2020) Hidden Long-Distance Movements by a Migratory Bird. Curr Biol
- 564 30:4056-4062.e3. https://doi.org/10.1016/j.cub.2020.07.056

- 565 Cox, A.S. and Kesler, D.C., 2012. Reevaluating the cost of natal dispersal: post-fledging survival of
   566 red-bellied woodpeckers. *The Condor*, *114*(2), pp.341-347.
- 567 Cranmer A, Smetzer JR, Welch L, Baker E (2017) A Markov model for planning and permitting
- 568 offshore wind energy: A case study of radio-tracked terns in the Gulf of Maine, USA. J Environ
- 569 Manage 193:400–409. https://doi.org/10.1016/j.jenvman.2017.02.010
- 570 Crewe TL, Kendal D, Campbell HA (2020) Motivations and fears driving participation in collaborative
- 571 research infrastructure for animal tracking. PLoS One 15:1–16.
- 572 https://doi.org/10.1371/journal.pone.0241964
- 573 Day, G., Fox, G., Hipperson, H., Maher, K., Tucker, R., Horsburgh, G., Waters, D., Durrant, K.L.,
- 574 Arnold, K., Burke, T. and Slate, J., 2023. Revealing the Demographic History of the European
- 575 nightjar (Caprimulgus europaeus). *Authorea Preprints*.
- 576 Delingat, J., Bairlein, F. and Hedenström, A., 2008. Obligatory barrier crossing and adaptive fuel
- 577 management in migratory birds: the case of the Atlantic crossing in Northern Wheatears
  578 (Oenanthe oenanthe). *Behavioral Ecology and Sociobiology*, *62*, pp.1069-1078.
- 579 DeMars, C.A., Johnson, C.J., Dickie, M., Habib, T.J., Cody, M., Saxena, A., Boutin, S. and Serrouya,
- 580 R., 2023. Incorporating mechanism into conservation actions in an age of multiple and emerging
- 581 threats: The case of boreal caribou. *Ecosphere*, *14*(7), p.e4627. Dhanjal-Adams KL, Klaassen
- 582 M, Nicol S, et al (2017) Setting conservation priorities for migratory networks under uncertainty.
- 583 Conserv Biol 31:646–656. https://doi.org/10.1111/cobi.12842
- 584 Doerr ED, Doerr VAJ (2005) Dispersal range analysis: Quantifying individual variation in dispersal
   585 behaviour. Oecologia 142:1–10. https://doi.org/10.1007/s00442-004-1707-z
- 586 Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry,
- 587 L.E., Burns, E.L., Edworthy, A. and Evans, M.J., 2014. The trajectory of dispersal research in
  588 conservation biology. Systematic review. PloS one, 9(4), p.e95053.
- 589 Du Feu, C.R., Clark, J.A., Schaub, M., Fiedler, W. and Baillie, S.R., 2016. The EURING Data Bank–a 590 critical tool for continental-scale studies of marked birds. *Ringing & Migration*, *31*(1), pp.1-18.
- 591 Dufour P, de Franceschi C, Doniol-Valcroze P, et al (2021) A new westward migration route in an

- 592 Asian passerine bird. Curr Biol 31:5590-5596.e4. https://doi.org/10.1016/j.cub.2021.09.086
- 593 Dufour P, Åkesson S, Hellström M, et al (2022) The Yellow-browed Warbler (Phylloscopus inornatus)
- as a model to understand vagrancy and its potential for the evolution of new migration routes.
- 595 Mov Ecol 10:1–15. https://doi.org/10.1186/s40462-022-00345-2
- 596 Dufour P, Lees AC, Gilroy J, Crochet P (2023) The overlooked importance of vagrancy in ecology and
- 597 evolution. Trends Ecol Evol xx:3–6. https://doi.org/10.1016/j.tree.2023.10.001
- 598 Endriss SB, Vahsen ML, Bitume E V., et al (2019) The importance of growing up: juvenile
- 599 environment influences dispersal of individuals and their neighbours. Ecol Lett 22:45–55.
- 600 https://doi.org/10.1111/ele.13166
- 601 Eng, M. L., et al. (2019). "A neonicotinoid insecticide reduces fueling and delays migration in
- 602 songbirds." Science 365(6458): 1177-1180
- Engels S, Schneider NL, Lefeldt N, et al (2014) Anthropogenic electromagnetic noise disrupts
- 604 magnetic compass orientation in a migratory bird. Nature 509:353–356.
- 605 https://doi.org/10.1038/nature13290
- 606 Evans DR (2018) The post-fledging survival and movements of juvenile Barn Swallows (*Hirundo*
- 607 *rustica*): an automated telemetry approach. 1–123
- Evans DR, Hobson KA, Kusack JW, et al (2020) Individual condition, but not fledging phenology,
- 609 carries over to affect post-fledging survival in a Neotropical migratory songbird. Ibis (Lond 1859)
- 610 162:331–344. https://doi.org/10.1111/ibi.12727
- 611 Fattorini N, Costanzo A, Romano A, et al (2023) Eco-evolutionary drivers of avian migratory
- 612 connectivity. Ecol Lett 1095–1107. https://doi.org/10.1111/ele.14223
- 613 Fiedler, W., 2009. New technologies for monitoring bird migration and behaviour. Ringing &
- 614 *Migration*, 24(3), pp.175-179. Flack A, Aikens EO, Kölzsch A, et al (2022) New frontiers in bird
- 615 migration research. Curr Biol 32:R1187–R1199. https://doi.org/10.1016/j.cub.2022.08.028
- 616 Frick, W.F., Kingston, T. and Flanders, J., 2020. A review of the major threats and challenges to
- 617 global bat conservation. Annals of the new York Academy of Sciences, 1469(1), pp.5-25.
- 618 Gauld, J.G., Silva, J.P., Atkinson, P.W., Record, P., Acácio, M., Arkumarev, V., Blas, J., Bouten, W.,

- Burton, N., Catry, I. and Champagnon, J., 2022. Hotspots in the grid: Avian sensitivity and
  vulnerability to collision risk from energy infrastructure interactions in Europe and North Africa.
  Journal of Applied Ecology, 59(6), pp.1496-1512.
- 622 Gómez C, Bayly NJ, Rosenberg K V. (2014) Fall stopover strategies of three species of thrush (
- 623 Catharus ) in northern South America . Auk 131:702–717. https://doi.org/10.1642/auk-14-56.1
- 624 Gómez C, Hobson KA, Bayly NJ, et al (2021) Migratory connectivity then and now: A northward shift
- 625 in breeding origins of a long-distance migratory bird wintering in the tropics. Proc R Soc B Biol
  626 Sci 288:. https://doi.org/10.1098/rspb.2021.0188
- 627 Goymann, W., Spina, F., Ferri, A. and Fusani, L., 2010. Body fat influences departure from stopover
  628 sites in migratory birds: evidence from whole-island telemetry. *Biology letters*, *6*(4), pp.478-481.
- Gregory KA, Francesiaz C, Jiguet F, Besnard A (2023) A synthesis of recent tools and perspectives in
   migratory connectivity studies. Mov Ecol 1–16. https://doi.org/10.1186/s40462-023-00388-z
- Griffin AS, Brown C, Woodworth BK, et al (2020) A large-scale automated radio telemetry network for
   monitoring movements of terrestrial wildlife in Australia. Aust Zool 40:379–391.
- 633 https://doi.org/10.7882/AZ.2019.026
- 634 Guilherme JL, Jones VR, Catry I, et al (2023) Connectivity between countries established by landbirds
- and raptors migrating along the African–Eurasian flyway. Conserv Biol 37:1–14.
- 636 https://doi.org/10.1111/cobi.14002
- 637 Hawkes Will L., Doyle Toby, Massy Richard, Weston Scarlett T., Davies Kelsey, Cornelius Elliott,
- 638 Collier Connor, Chapman Jason W., Reynolds Don R. and Wotton Karl R. 2024The most
- 639 remarkable migrants—systematic analysis of the Western European insect flyway at a Pyrenean
- 640 mountain passProc. R. Soc. B.29120232831 http://doi.org/10.1098/rspb.2023.2831
- Hayes, S., Boyd, B.P. and Stutchbury, B.J., 2024. Why do juvenile Wood Thrushes make long-
- 642 distance pre-migratory movements across a fragmented landscape?. Journal of Field643 Ornithology, 95(2).
- Hedenström, A., 2008. Adaptations to migration in birds: behavioural strategies, morphology and
  scaling effects. Philosophical Transactions of the Royal Society B: Biological Sciences,

646 363(1490), pp.287-299.

- Hegemann A, Alcalde Abril P, Sjöberg S, et al. 2018. A mimicked bacterial infection prolongs stopover
  duration in songbirds—but more pronounced in short- than long-distance migrants. J Anim Ecol.;
  87: 1698–1708. https://doi.org/10.1111/1365-2656.12895
- Hewson, C.M., Thorup, K., Pearce-Higgins, J.W. and Atkinson, P.W., 2016. Population decline is
- 651 linked to migration route in the Common Cuckoo. *Nature Communications*, 7(1), p.12296.
- Hiemer, D., Salewski, V., Fiedler, W., Hahn, S. and Lisovski, S., 2018. First tracks of individual
  Blackcaps suggest a complex migration pattern. *Journal of ornithology*, *159*, pp.205-210.
- Hirschhofer, S., Liechti, F., Ranacher, P., Weibel, R. and Schmid, B., 2023. High-intensity bird
- 655 migration along Alpine valleys calls for protective measures against anthropogenically induced 656 avian mortality. Remote Sensing in Ecology and Conservation.
- Horton KG, Buler JJ, Anderson SJ, et al (2023) Artificial light at night is a top predictor of bird
  migration stopover density. Nat Commun 14:1–11. https://doi.org/10.1038/s41467-023-43046-z
- Horton KG, La Sorte FA, Sheldon D, et al (2020) Phenology of nocturnal avian migration has shifted
  at the continental scale. Nat Clim Chang 10:63–68. https://doi.org/10.1038/s41558-019-0648-9
- 661 Howard C, Stephens PA, Pearce-Higgins JW, et al (2020) Disentangling the relative roles of climate
- and land cover change in driving the long-term population trends of European migratory birds.
- 663 Divers Distrib 26:1442–1455. https://doi.org/10.1111/ddi.13144
- Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N. and Chapman, J.W., 2016. Mass
  seasonal bioflows of high-flying insect migrants. Science, 354(6319), pp.1584-1587.
- 666 Iler, A.M., CaraDonna, P.J., Forrest, J.R. and Post, E., 2021. Demographic consequences of
- 667 phenological shifts in response to climate change. Annual Review of Ecology, Evolution, and
  668 Systematics, 52, pp.221-245.
- 669 Imlay TL, Saldanha S, Taylor PD (2020) The fall migratory movements of bank swallows, riparia
- 670 riparia: Fly-and-forage migration? Avian Conserv Ecol 15:1–11. https://doi.org/10.5751/ACE-
- 671 01463-150102
- Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A.,

- 673 Jacob, U., Takahashi, Y., Settele, J. and Díaz, S., 2022. The direct drivers of recent global
- 674 anthropogenic biodiversity loss. Science advances, 8(45), p.eabm9982.
- Jiguet F, Robert A, Lorrillière R, Hobson KA, Kardynal KJ, Arlettaz R, Bairlein F, Belik V, Bernardy P,
- 676 Copete JL et al: Unravelling migration connectivity reveals unsustainable hunting of the declining
  677 ortolan bunting. Science Advances 2019, 5(5):eaau2642.
- Knight, S.M., Pitman, G.M., Flockhart, D.T. and Norris, D.R., 2019. Radio-tracking reveals how wind
  and temperature influence the pace of daytime insect migration. *Biology letters*, *15*(7),
  p.20190327.
- Lagerveld, S., Jonge Poerink, B., Haselager, R., & Verdaat, H. (2014). Bats in Dutch offshore wind
  farms in autumn 2012. Lutra, 57, 61–69
- Lagerveld, S., Wilkes, T., van Puijenbroek, M.E., Noort, B.C. and Geelhoed, S.C., 2023. Acoustic
- 684 monitoring reveals spatiotemporal occurrence of Nathusius' pipistrelle at the southern North Sea
  685 during autumn migration. *Environmental Monitoring and Assessment*, *195*(9), p.1016.
- Lamb JS, Loring PH, Paton PWC (2023) Distributing transmitters to maximize population-level
- 687 representativeness in automated radio telemetry studies of animal movement. Mov Ecol 11:1–
- 688 12. https://doi.org/10.1186/s40462-022-00363-0
- Lameris, T. K., et al. (2018). "Arctic Geese Tune Migration to a Warming Climate but Still Suffer from
  a Phenological Mismatch." Current Biology 28(15): 2467-2473.e2464.
- le Roux CE, Nocera JJ (2021) Roost sites of chimney swift (Chaetura pelagica) form large-scale
  spatial networks. Ecol Evol 11:3820–3829. https://doi.org/10.1002/ece3.7235
- 693 Lefevre KL, Smith AD (2020) Florida's strategic position for collaborative automated telemetry
- tracking of avian movements across the Americas. J Fish Wildl Manag 11:369–375.
- 695 https://doi.org/10.3996/082019-JFWM-068
- Lerche-Jørgensen, M., Willemoes, M., Tøttrup, A.P., Snell, K.R.S. and Thorup, K., 2017. No apparent
- 697 gain from continuing migration for more than 3000 kilometres: willow warblers breeding in
- 698 Denmark winter across the entire northern Savannah as revealed by geolocators. *Movement*
- 699 *Ecology*, *5*, pp.1-7.

- 700 Lin HY, Schuster R, Wilson S, et al (2020) Integrating season-specific needs of migratory and
- 701 resident birds in conservation planning. Biol Conserv 252:108826.
- 702 https://doi.org/10.1016/j.biocon.2020.108826
- Linhart, R.C., Hamilton, D.J., Paquet, J. and Gratto-Trevor, C.L., 2023. Evidence of differing staging
- strategies between adult and juvenile Semipalmated Sandpipers highlights the importance of
- small staging sites in Atlantic Canada. Ornithology, 140(1), p.ukac056. Liu J, Lei W, Mo X, et al
- 706 (2022) Unravelling the processes between phenotypic plasticity and population dynamics in
- 707 migratory birds. J Anim Ecol 91:983–995. https://doi.org/10.1111/1365-2656.13686
- López-López P (2016) Individual-Based Tracking Systems in Ornithology: Welcome to the Era of Big
   Data. Ardeola 63:103–136. https://doi.org/10.13157/arla.63.1.2016.rp5
- Loring, P.H., Paton, P.W.C., McLaren, J.D., Bai, H., Janaswamy, R., Goyert, H.F., Griffin, C.R. and
- 711 Sievert, P.R., 2019. Tracking offshore occurrence of common terns, endangered roseate terns, and
- 712 threatened piping plovers with VHF arrays. Sterling (VA): US Department of the Interior, Bureau of
- 713 Ocean Energy Management. OCS Study BOEM, 17, p.140.
- 714 Madsen, J., Schreven, K.H., Jensen, G.H., Johnson, F.A., Nilsson, L., Nolet, B.A. and Pessa, J.,
- 715 2023. Rapid formation of new migration route and breeding area by Arctic geese. *Current*
- 716 *Biology*, 33(6), pp.1162-1170.
- 717 Marchand CB, Desrochers A, Tremblay JA, Côté P (2020) Comparing fall migration of three Catharus
- 718 species using a radio-telemetry network. Anim Migr 7:1–8. https://doi.org/10.1515/ami-2020-0001
- 719 Marques, A.T., Batalha, H. and Bernardino, J., 2021. Bird displacement by wind turbines: assessing
- 720 current knowledge and recommendations for future studies. Birds, 2(4), pp.460-475.
- Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E. and Tonra, C.M., 2015. A call for full annual cycle
  research in animal ecology. *Biology letters*, *11*(8), p.20150552.
- Martell, M.S., Archer, A.A., Burnette, A., Lee, M., Nicoletti, F. and Hall, K.A., 2023. Using the Motus
  system to track post-breeding dispersal of American Kestrels nesting in Minnesota,
- 725 USA. Journal of Raptor Research, 57(2), pp.154-163.
- 726 Masero, J.A., Santiago-Quesada, F., Sanchez-Guzman, J.M., Villegas, A., Abad-Gomez, J.M., Lopes, R.J.,

- Encarnacao, V., Corbacho, C. and Moran, R., 2011. Long lengths of stay, large numbers, and trends
  of the Black-tailed Godwit Limosa limosa in rice fields during spring migration. *Bird Conservation International*, *21*(1), pp.12-24.
- Matthysen, E. and Clobert, J., 2012. Multicausality of dispersal: a review. Dispersal ecology and
  evolution, 27, pp.3-18.
- 732 Mckinnon EA, Laplante MP, Love OP, et al (2019) Tracking Landscape-Scale Movements of Snow
- 733 Buntings and Weather-Driven Changes in Flock Composition During the Temperate Winter.
- 734 Front Ecol Evol 7:1–11. https://doi.org/10.3389/fevo.2019.00329
- 735 McKinnon EA, Love OP (2018) Ten years tracking the migrations of small landbirds: Lessons learned
- in the golden age of bio-logging. Auk: Orntihological Advances 135 (4):834–856.
- 737 https://doi.org/10.1642/AUK-17-202.1
- McLaren JD, Buler JJ, Schreckengost T, et al (2018) Artificial light at night confounds broad-scale
  habitat use by migrating birds. Ecol Lett 21:356–364. https://doi.org/10.1111/ele.12902
- 740 Mitchell GW, Woodworth BK, Taylor PD, Norris DR (2015) Automated telemetry reveals age specific
- 741 differences in flight duration and speed are driven by wind conditions in a migratory songbird.
- 742 Mov Ecol 3:1–13. https://doi.org/10.1186/s40462-015-0046-5
- 743 Morales JM, Moorcroft PR, Matthiopoulos J, et al (2010) Building the bridge between animal
- 744 movement and population dynamics. Philos Trans R Soc B Biol Sci 365:2289–2301.
- 745 https://doi.org/10.1098/rstb.2010.0082
- 746 Morrison CA, Robinson RA, Butler SJ, et al (2016) Demographic drivers of decline and recovery in an

747 Afro-Palaearctic migratory bird population. Proc R Soc B Biol Sci 283:.

- 748 https://doi.org/10.1098/rspb.2016.1387
- 749 Mukhin, A., Kosarev, V. and Ktitorov, P., 2005. Nocturnal life of young songbirds well before
- 750 migration. *Proceedings of the Royal Society B: Biological Sciences*, 272(1572), pp.1535-1539.
- 751 Mukhin A, Kobylkov D, Kishkinev D, Grinkevich V (2018) Interrupted breeding in a songbird migrant
- 752 triggers development of nocturnal locomotor activity. Sci Rep 8:1–8.
- 753 https://doi.org/10.1038/s41598-018-23834-0

- 754 Nadal J, Ponz C, Margalida A, Pennisi L (2020) Ecological markers to monitor migratory bird
- 755 populations: Integrating citizen science and transboundary management for conservation
- 756 purposes. J Environ Manage 255:109875. https://doi.org/10.1016/j.jenvman.2019.109875
- 757 Nadal J, Sáez D, Margalida A (2022) Crossing artificial obstacles during migration: The relative global
- 758 ecological risks and interdependencies illustrated by the migration of common quail Coturnix
- 759 coturnix. Sci Total Environ 808:. https://doi.org/10.1016/j.scitotenv.2021.152173
- Niebuhr BBS, Wosniack ME, Santos MC, et al (2015) Survival in patchy landscapes: The interplay
  between dispersal, habitat loss and fragmentation. Sci Rep 5:1–10.
- 762 https://doi.org/10.1038/srep11898
- 763 Nilsson C, Dokter AM, Verlinden L, et al (2019) Revealing patterns of nocturnal migration using the
- European weather radar network. Ecography (Cop) 42:876–886.
- 765 https://doi.org/10.1111/ecog.04003
- Nussbaumer, R., Gravey, M., Briedis, M. and Liechti, F., 2023. Global positioning with animal-borne
   pressure sensors. Methods in Ecology and Evolution, 14(4), pp.1104-1117.
- Patchett, R., Finch, T. and Cresswell, W., 2018. Population consequences of migratory variability
  differ between flyways. *Current Biology*, *28*(8), pp.R340-R341.
- Reichlin, T.S., Schaub, M., Menz, M.H., Mermod, M., Portner, P., Arlettaz, R. and Jenni, L., 2009.
  Migration patterns of Hoopoe Upupa epop s and Wryneck Jynx torquilla: an analysis of
- European ring recoveries. Journal of Ornithology, 150, pp.393-400.
- 773 Rigal, S., Dakos, V., Alonso, H., Auniņš, A., Benkő, Z., Brotons, L., Chodkiewicz, T., Chylarecki, P.,
- 774 De Carli, E., Del Moral, J.C. and Domşa, C., 2023. Farmland practices are driving bird
- population decline across Europe. *Proceedings of the National Academy of Sciences*, *120*(21),
  p.e2216573120.
- Rueda-Uribe, C., Lötberg, U. and Åkesson, S., 2022. Foraging on the wing for fish while migrating
  over changing landscapes: traveling behaviors vary with available aquatic habitat for Caspian
  terns. *Movement ecology*, *10*(1), p.9.
- 780 Ruegg KC, Anderson EC, Paxton KL, et al (2014) Mapping migration in a songbird using high-

- 781 resolution genetic markers. Mol Ecol 23:5726–5739. https://doi.org/10.1111/mec.12977
- Rüppel G, Hüppop O, Lagerveld S, Schmaljohann H, Brust V. 2023. Departure, routing and landing
  decisions of long distance migratory songbirds in relation to weather. R. Soc. Open Sci. 10:
  221420. https://doi.org/10.1098/rsos.221420
- 785 Sala, O.E., Stuart Chapin, F.I.I.I., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald,
- 786 E., Huenneke, L.F., Jackson, R.B., Kinzig, A. and Leemans, R., 2000. Global biodiversity

787 scenarios for the year 2100. Science, 287(5459), pp.1770-1774.

- Saracco, J.F., Desante, D.F. and Kaschube, D.R., 2008. Assessing landbird monitoring programs and
   demographic causes of population trends. The Journal of Wildlife Management, 72(8), pp.1665 1673.
- Saura, S., Bodin, Ö. and Fortin, M.J., 2014. EDITOR'S CHOICE: Stepping stones are crucial for
   species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, *51*(1), pp.171-182.
- Sawyer, H., Kauffman, M.J., Nielson, R.M. and Horne, J.S., 2009. Identifying and prioritizing ungulate
   migration routes for landscape-level conservation. *Ecological Applications*, *19*(8), pp.2016-2025.
- Schmaljohann, H., Liechti, F., Bächler, E., Steuri, T. & Bruderer, B. 2008 Quantification of bird
  migration by radar a detection probability problem. Ibis 150, 342-355.
- Schmaljohann H (2020) Radar aeroecology a missing piece of the puzzle for studying the migration
   ecology of animals. Ecography (Cop) 43:236–238. https://doi.org/10.1111/ecog.04807
- 800 Schmaljohann H, Klinner T (2020) A quasi-experimental approach using telemetry to assess
- 801 migration-strategy-specific differences in the decision-making processes at stopover. BMC Ecol
- 802 20:1–12. https://doi.org/10.1186/s12898-020-00307-5
- Schmaljohann, H., Eikenaar, C. and Sapir, N., 2022. Understanding the ecological and evolutionary
  function of stopover in migrating birds. *Biological Reviews*, 97(4), pp.1231-1252.
- Schorcht, W., Bontadina, F. and Schaub, M., 2009. Variation of adult survival drives population
  dynamics in a migrating forest bat. Journal of Animal Ecology, 78(6), pp.1182-1190.

- 807 Serratosa, J., Oppel, S., Rotics, S., Santangeli, A., Butchart, S.H., Cano-Alonso, L.S., Tellería, J.L.,
- 808 Kemp, R., Nicholas, A., Kalvāns, A. and Galarza, A., 2024. Tracking data highlight the
- 809 importance of human-induced mortality for large migratory birds at a flyway scale. *Biological*810 *Conservation*, 293, p.110525.
- 811 Sharma, A., Sur, S., Tripathi, V. and Kumar, V., 2023. Genetic control of avian migration: insights
  812 from studies in latitudinal passerine migrants. *Genes*, *14*(6), p.1191.
- Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T., & Muheim, R. (2015).
  Weather and fuel reserves determine departure and flight decisions in passerines migrating
  across the Baltic Sea. Animal Behaviour, 104, 59-68.
- 816 Smetzer, J.R. and King, D.I., 2018. Prolonged stopover and consequences of migratory strategy on
- 817 local-scale movements within a regional songbird staging area. *The Auk: Ornithological*
- 818 Advances, 135(3), pp.547-560.
- Smith, R.A., Gagné, M. and Fraser, K.C., 2021. Pre-migration artificial light at night advances the
  spring migration timing of a trans-hemispheric migratory songbird. *Environmental Pollution*, 269,
  p.116136.
- 822 Snell KRS, Stokke BG, Moksnes A, et al (2018) From Svalbard to Siberia: Passerines breeding in the
- High Arctic also endure the extreme cold of the Western Steppe. PLoS One 13:1–14.
- 824 https://doi.org/10.1371/journal.pone.0202114
- 825 Soulsbury, C., Gray, H., Smith, L., Braithwaite, V., Cotter, S., Elwood, R.W., Wilkinson, A. and Collins,
- L.M., 2020. The welfare and ethics of research involving wild animals: A primer. *Methods in Ecology and Evolution*, *11*(10), pp.1164-1181.
- Taylor PD, Crewe TL, Mackenzie SA, et al (2017) The Motus Wildlife Tracking System: a collaborative
   research network. Avian Conserv Ecol 12:8
- 830 Taylor PD, Mackenzie SA, Thurber BG, et al (2011) Landscape movements of migratory birds and
- bats reveal an expanded scale of stopover. PLoS One 6:.
- 832 https://doi.org/10.1371/journal.pone.0027054
- 833 Thorup K, Ortvad TE, Holland RA, et al (2012) Orientation of vagrant birds on the Faroe Islands in the

- 834 Atlantic Ocean. J Ornithol 153:1261–1265. https://doi.org/10.1007/s10336-012-0883-6
- Thorup, K., Korner-Nievergelt, F., Cohen, E.B. and Baillie, S.R., 2014. Large-scale spatial analysis of
  ringing and re-encounter data to infer movement patterns: A review including methodological
- 837 perspectives. *Methods in Ecology and Evolution*, *5*(12), pp.1337-1350.
- 838 Travis JMJ, Dytham C (2013) Dispersal and climate change: a review of theory. Dispersal Ecol Evol
- 839 337–348. https://doi.org/10.1093/acprof:oso/9780199608898.003.0026
- 840 Turbek SP, Scordato ESC, Safran RJ (2018) The Role of Seasonal Migration in Population
- 841 Divergence and Reproductive Isolation. Trends Ecol Evol 33:164–175.
- 842 https://doi.org/10.1016/j.tree.2017.11.008
- 843 United Nations Environment Programme (UNEP) 2020. Convention on Migratory Species (CMS)
- Resolution 12.6 (Rev. COP13): Improving ways of addressing connectivity in the conservation of
  migratory species.
- 846 https://www.cms.int/sites/default/files/document/cms\_cop13\_res.12.26\_rev.cop13\_e.pdf
- van Doren BM, Willard DE, Hennen M, et al (2021) Drivers of fatal bird collisions in an urban center.

848 Proc Natl Acad Sci U S A 118:. https://doi.org/10.1073/pnas.2101666118

- 849 Vickery JA, Mallord JW, Adams WM, et al (2023) The conservation of Afro-Palaearctic migrants :
- 850 What we are learning and what we need to know? https://doi.org/10.1111/ibi.13171
- 851 Weisshaupt N, Lehtiniemi T, Koistinen J (2021) Combining citizen science and weather radar data to

study large-scale bird movements. Ibis (Lond 1859) 163:728–736.

- 853 https://doi.org/10.1111/ibi.12906
- Wikelski, M., Kays, R.W., Kasdin, N.J., Thorup, K., Smith, J.A. and Swenson Jr, G.W., 2007. Going
- wild: what a global small-animal tracking system could do for experimental biologists. Journal of
  Experimental Biology, 210(2), pp.181-186.
- 857 Wilcox, A.A., Newman, A.E., Raine, N.E., Mitchell, G.W. and Norris, D.R., 2021. Effects of early-life
- 858 exposure to sublethal levels of a common neonicotinoid insecticide on the orientation and
- 859 migration of monarch butterflies (Danaus plexippus). Journal of Experimental Biology, 224(4),
- 860 p.jeb230870.

861 Wilcover & Wikelski 2008

Willmott, J.R., Forcey, G. and Vukovich, M., 2023, May. New insights into the influence of turbines on
the behaviour of migrant birds: implications for predicting impacts of offshore wind developments
on wildlife. In *Journal of Physics: Conference Series* (Vol. 2507, No. 1, p. 012006). IOP

865 Publishing.

Woodworth BK, Mitchell GW, Norris DR, et al (2015) Patterns and correlates of songbird movements
at an ecological barrier during autumn migration assessed using landscape- and regional-scale
automated radiotelemetry. Ibis (Lond 1859) 157:326–339. https://doi.org/10.1111/ibi.12228

Zaugg, S., Saporta, G., van Loon, E., Schmaljohann, H. & Liechti, F. 2008 Automatic identification of

870 bird targets with radar via patterns produced by wing flapping. Journal of the Royal Society Interface

**871** 5, 1041-1053.

872 Zenzal TJ, Ward MP, Diehl RH, et al (2021) Retreat, detour or advance? Understanding the

873 movements of birds confronting the Gulf of Mexico. Oikos 130:739–752.

874 https://doi.org/10.1111/oik.07834

875 Zurell D, Graham CH, Gallien L, et al (2018) Long-distance migratory birds threatened by multiple

independent risks from global change. Nat Clim Chang 8:992–996.

877 https://doi.org/10.1038/s41558-018-0312-9

Züst Z, Mukhin A, Taylor PD, Schmaljohann H (2023) Pre-migratory flights in migrant songbirds: the

879 ecological and evolutionary importance of understudied exploratory movements. Mov Ecol 11:1-

880 15. https://doi.org/10.1186/s40462-023-00440-y

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Figure 1: 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.

887 Orange 'wifi' symbols represent transmission capability.



#### 889

890 Figure 2a. 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 (6m height), with 4 six-

892 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 3: 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.



## 901 902 903 904

Figure 4: 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 905 bats; b: examples of potential station placement (yellow dots) and data collection at Gibraltar, Iberian 906 peninsula, where many thousands of migratory species will cross an important migratory barrier, the

907 Mediterranean Sea. Blue arrows exemplify expected flight paths that could be detected by the set-up.