- 1 Mapping migratory routes: Avian conservation-focused
- 2 opportunities for a pan-European automated telemetry network
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- 29 We identify how demographic knowledge gaps in the conservation of migratory
- 30 species can be filled using Motus automated VHF telemetry.

32 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 40 41 required to adequately monitor changes in the migratory and demographic 42 processes of populations during all parts of the annual cycle. The Motus Wildlife 43 Tracking System (Motus) could provide a solution to data gaps that exist for small, migratory species. Motus is an automated telemetry system for animal tracking, 44 which provides a collaborative network by using a single VHF radio frequency for all 45 tracked individuals, in combination with an individual tag identifier. Motus can provide 46 information on movements made by individuals of small migrant species, thus aiding 47 our understanding of aspects of their migration that could impact demographic 48 49 parameters.

50 Here we describe conservation-focused research opportunities, with a 51 particular lense on small European migrant birds. We highlight examples from the 52 existing network, and identify geographical gaps which, if filled, could track continent-53 wide movements. We conclude that Motus is a useful tool to produce individual-level 54 migration information for a variety of small-bodied taxa, and that a drive to expand 55 the network will improve its ability to direct conservation plans for such species.

56

57 Introduction

Biodiversity loss driven by land use change, exploitation of natural resources, 58 and affected further by climatic disruption, is a defining feature of the Anthropocene 59 (Sala et al. 2000). A decline in habitat availability and disruption to ecosystem 60 structure, reducing critical services such as nutrient cycling, carbon storage and 61 62 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 63 physical changes, i.e. habitat loss, but also through increases in zoonotic and vector-64 borne diseases (Jaurequiberry et al. 2022), and pest outbreaks (Ayres and 65 Lombardero 2018). These impacts affect species' distributions, abundances, fitness, 66 67 and consequently their ability to complete their life cycle successfully (Bellard et al. 2012). 68

Of particular concern are migratory species, which serve as ecological 69 indicators and providers of vital contributions to ecosystem functioning, including 70 71 biomass production, pollination, and pest control (Bauer and Hoye 2014, Satterfield et al. 2020). Migratory species experience a variety of environmental conditions on 72 73 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 74 configuration, throughout their annual cycle, can mean that their requirements for 75 76 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 77 78 (Jiguet et al. 2019), the extension and complication of ecological barriers (Gauld et al. 2022), as well as increasingly unpredictable climatic patterns decoupling the 79 phenology of ecologically linked species (ller et al. 2021, Clarke et al. 2022). 80

81 These challenges directly conflict with the multi-factorial optimisation of migration, which is often based on inherited, integrated migration strategies 82 (Åkesson and Helm 2020; Schmaljohann et al. 2022, Fattorini et al. 2023). While 83 migrant species differ in their migratory timing, distance, speed, and route, their 84 journeys all involve repeated, alternating migratory endurance flights and stopover 85 periods for resting, recovering and fuelling (Alerstam et al. 2003; Åkesson and 86 87 Hedenström 2007; Schmaljohann et al. 2022). Understanding the factors impacting population trends of these species, i.e., the changes in vital rates that drive 88 89 population growth or decline, is essential (Morrison et al. 2016), as many migratory species cannot respond to changes at a sufficiently rapid pace, producing 90 widespread population declines (Both et al. 2006, Wilcover & Wikelski 2008, Frick et 91 92 al. 2020, Rosenberg et al. 2019, Vickery et al. 2023).

The Convention on the Conservation of Migratory Species highlights the need 93 94 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. 95 2023, Vickery et al. 2023). However, gathering data from a sufficiently high number 96 of individuals from different populations at this scale, is extremely challenging 97 98 (Morrison et al. 2016; McKinnon and Love 2018), and reliant on international 99 collaboration (Nadal et al. 2020; Vickery et al. 2023, Serratosa et al. 2024). 100 Particularly for small and light migratory passerines, waders and highly aerial 101 species such as swifts, their size and behaviour have rendered it difficult to study their movements (Wikelski et al. 2007, Fiedler 2009). 102

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105 Current methods and their limitations

106 Studying when and where differences in population processes occur in 107 migratory birds is notoriously difficult (Doerr and Doerr 2005; Border et al. 2017, 108 Telensky et al. 2020). However, quantifying variation in survival, mortality, emigration 109 and immigration (summarized as dispersal), is crucially important to formulate 110 effective conservation measures for populations and species that are at risk of 111 decline (Gómez et al. 2021, DeMars et al. 2023).

112 Currently, we have little detailed spatial and temporal information on migrating 113 small birds. Broad scale migration patterns across Europe, including concentrations 114 of both avian and insect migrants passing through marine and mountainous regions, have been identified using radar (Bruderer & Jenni 1990, Bruderer & Liechti 1999, 115 Nilsson et al. 2019, Weisshaupt et al. 2021, Hirschhofer et al. 2024). Yet radar data 116 117 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 118 119 facilitate links to demography, physiology and ecology.

120 In contrast, several million individuals have been marked using metal or 121 colour rings across Europe (Du Feu et al. 2016, Spina et al. 2022), contributing to 122 our fundamental knowledge of bird movements. Yet recapture, recovery, and resighting probabilities are largely low (across 32 European level ringing schemes, 123 124 recovery rate for all species combined varied from 0.6 - 7.6%; Baillie 1995). This is 125 particularly the case on the wintering grounds but is highly variable amongst species 126 and locations (Thorup et al. 2014). For example, the Willow Warbler (*Phylloscopus* 127 trochilis) is ringed in huge numbers on its breeding ground in northern Europe, but 128 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).

131 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), 132 and nomadic, non-breeding movements (Snell et al. 2018; Mckinnon et al. 2019). 133 134 However, individual tracking of small migrants requires tracking devices weighing a 135 maximum 3-5 % of an individual's body weight (Barron et al. 2010), which excludes 136 most tracking technology on the market (Figure 1; Bridge et al. 2011, McKinnon & 137 Love 2018), including new low-power, wide area devices such as SigFox or 138 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-139 140 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 141 142 radio-tracking systems, e.g., the tRackIT System and the ATLAS project, have 143 narrow spatial coverage and a limit on how many individuals (c. 200) they can 144 monitor concurrently (Gottwald et al. 2019, Beardsworth et al. 2022).

145 The Motus Wildlife Tracking System (Motus) exploits a network of VHF receiving stations aligned on the same frequency, which continuously receive and 146 147 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, 148 we focus on filling conservation and demographic-specific knowledge gaps using 149 150 Motus to track migratory birds, and we hope to further spark the collaborative spirit of 151 Motus to create a denser network in Europe and resemble the situation in North America. 152

153 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, <u>Resolution 12.26)</u> 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 180 181 Europe, and there is a lack of a universally-permitted tracking frequency, so does not 182 yet allow continuous tracking across the continent. In many European countries, the 183 frequency of 150.1 MHz is authorised either temporarily or permanently for wild 184 animal telemetry tracking. Multi-frequency detection by Motus receivers is possible. 185 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 186 approximately €80 – 300 per station, for an additional 1 - 4 antennas, plus the extra 187 188 cost of cables. For the tags, researchers can select from among a number of options 189 and device parameters, including burst interval (usually from 1 s to 1 min), battery or 190 solar power, attachment and antenna type, in line with their specific scientific 191 requirements (Figure 1).

192 Motus has many promising features, including its extended temporal and 193 spatial data gathering capacity, compared to standard radio-tracking. In addition to 194 autonomous, near-real-time recording of the receivers and sub-0.5 g tags, the spatial 195 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 196 tags have shown substantial improvements in positional accuracy (Nussbaumer et 197 198 al. 2023). Receiving stations can, in theory, be placed anywhere (see Figure 3b) and 199 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 200 201 (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 205 general. Most studies do not detect all of the individuals which are tagged; the 206 207 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. 208 (2020) reported rates closer to 50-70%, whereas a dense coverage of receivers on 209 210 the small island of Helgoland repeatedly resulted in detection rates of 95-100% 211 (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 212 213 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, 214 215 and the numbers required to cause this confusion mean this is unlikely to happen in a 'natural' scenario. 216

217 Motus is already producing important insights into the movements of migrating 218 and wintering European birds, including a better understanding of the migratory and pre-migratory movements of sea-crossing thrushes (Brust et al. 2019) and 219 220 differences between long and short distance migrants in stopover time and flight 221 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 222 223 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). 224

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

229 Survival and mortality

230 Despite the biological significance of survival and mortality on population size and its dynamics (Sandercock 2020), little is known about both rates in migratory 231 232 passerines. Within migratory species, variation in survival among populations can be 233 linked to alternative routes and their different pressures (Hewson et al. 2016). The latter may increase population-specific immediate and delayed fitness costs 234 (Dhanjal-Adams et al. 2017), which might be particularly prevailing in those areas 235 236 that support high numbers of 'co-migrants' (multiple species moving through major 237 sites and corridors simultaneously - Cohen et al. 2020). The convergence of 238 otherwise spatially segregated populations at single locations may also increase the 239 probability of disease transmission with delayed fitness costs (Cohen et al. 2020).

240 To obtain information on route- or area-specific mortality rates, focusing 241 receiving station placement in closely packed 'fence' or 'curtain' formation (Figure 4) 242 would provide 'checkpoints' for tagged migrants along their migratory routes. If there 243 are sufficient stations intersecting migratory routes (and adequate numbers of 244 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 245 246 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 247 248 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 249

high level of certainty, knowing that a high proportion of marked individuals had beendetected.

252 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 253 inform habitat protection and management on the wintering grounds. Motus has also 254 255 been used by Brunner et al. (2022) to identify high migratory connectivity amongst populations of the elusive Swainson's warbler (Limnothlypis swainsonii), which has 256 257 implications for population-specific changes and can direct future monitoring work. 258 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 259 the data, therefore reducing bias. Extensive testing of detection capability of an 260 261 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 262 263 (Cooper et al. 2024) and restricted temporal period to increase the robustness of the estimates (Evans et al. 2020, Bliss et al. 2020). 264

265 Identification of Stopover sites

Motus can be used in regional arrays that expand outwards from a known 266 stopover site, allowing identification of exploratory and regional movements by birds 267 that may be assessing the wider area, often undertaken at night (Taylor et al. 2011, 268 Brown and Taylor 2015, Schmaljohann & Eikenaar 2017). In Europe, this could build 269 on current ringing efforts at hotspots (e.g. Bay of Biscay; Strait of Gibraltar) but at 270 271 spatial scales not feasible for ringing. Pinpointing specific sites for targeted conservation efforts is important, where limited, localised stopover site use could 272 273 induce higher vulnerability in certain migrating species (Bayly et al. 2013, Gómez et 274 al. 2014, Hagelin et al. 2021).

275 Temporal information on arrival and departure time, using Motus on multiple 276 individuals of different species, can help with elucidating the functions of stopover sites (Moore 2018, Linscott and Senner 2021, Schmaljohann et al. 2022). 277 278 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 279 might even disappear completely (Bayly et al. 2018). Smetzer and King (2018) used 280 281 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 282 283 the United States. The prolonged stopovers recorded by both species suggest that 284 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. 285

286 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 287 288 variation in detection distance due to topography and the behaviour of the species 289 must be taken into account), to provide insights into how birds respond to such 290 barriers (e.g. Sjöberg et al. 2015, Zenzal et al. 2021). This might include local to 291 regional scale movements before crossing, intrinsic and extrinsic conditions required 292 for a successful crossing, stopover duration, departure directions, and potential 293 differences between populations and seasons. Both Holberton et al. (2019) and 294 Herbert et al. (2022) used Motus to demonstrate site-based variation in stopover 295 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 296 297 one or more stopover sites could have population level implications.

298 <u>Dispersal, immigration and emigration</u>

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).

304 Species with discrete breeding sites restricted by habitat may display genetic structure that could increase, and become inbred, with further habitat loss and 305 306 climate change without immigration (Day et al., 2023). These changes may 307 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 308 emigration (e.g. as in le Roux & Nocera 2021 using Motus on Chimney swifts) to 309 310 avoid loss of genetic diversity, is important for deciding what conservation measures 311 might be useful (Driscoll et al. 2014). We can estimate emigration and immigration 312 rates of a species of interest, through comprehensive tagging campaigns (ethical considerations of such projects notwithstanding; Soulsbury et al. 2020), where Motus 313 314 stations cover initial breeding sites, and at the same time the potential areas to where the birds might disperse. 315

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 feasibleusing this system.

324 Questions remain about the function of exploratory dispersal movements, which may be preparatory information gathering trips ('homing target' or 'habitat 325 optimization' hypotheses, Mitchell et al. 2015), or pre-migratory flights (Züst et al. 326 327 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 328 329 individuals during the dispersal phase can help us to understand the role of (long-330 distance) dispersal in the evolution of new migration routes and wintering grounds, 331 perhaps as part of the wider phenomenon of vagrancy (Lees & Gilroy 2009, Dufour et al. 2021, 2022). 332

333 Motus' ability to expand spatially and temporally beyond the capabilities of manual VHF tracking, thus reducing bias and monitoring 'hidden' movements (Züst 334 335 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 336 et al. 2024). Results from such studies can benefit practical conservation decisions 337 338 to improve our understanding of how far and in what direction juveniles disperse. Tracking of many different young individuals can also highlight how individual 339 340 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 341 might be affected by surrounding habitat quality (Wood thrush: Hayes et al. 2020). 342 These practical elements are invaluable to formulate effective conservation 343 measures and facilitate population stability (Travis and Dytham 2013; Niebuhr et al. 344 2015, Endriss et al. 2019). 345

346 <u>Understanding migratory decisions</u>

In addition to using the Motus network to describe migration, it can facilitate 347 an 'experimental' approach, i.e. extending laboratory-based studies in natural 348 scenarios (Goymann et al. 2010 and Schmaljohann and Klinner (2020). For instance, 349 350 by radio-tagging "lean" and "fat" individuals of a species on a single day to minimize 351 the effect of weather variation on the birds' departure decision (e.g. Karwinkel et al 352 2022, 2024). When numerous individuals subject to the same external conditions are 353 tracked at the same time, this may then allow estimation of conditions when most 354 individuals migrate (Delingat et al. 2008, Schmaljohann & Klinner 2020), for example 355 during favourable winds (Lagerveld et al. In Press).

356 Parameters derived from flights of individuals tracked with Motus such as 357 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), 358 359 can allow comparisons in behaviour among individuals of different populations, and 360 those that orient across and around barriers (Figure 5b; Schmaljohann & Naef-Daenzer 2011, Woodworth et al. 2015; Brust and Hüppop 2022). An improved 361 362 understanding of migration behaviour, its limitations and flexibility among different species, can help us to better predict how species might adapt to changes around 363 them and improve efforts towards their conservation (Sutherland 1998). 364

365 Obtaining individual responses to environmental stressors

366 Motus can also address identifiable conservation concerns, and detect
367 responses to specific forms of anthropogenic or environmental disruption.

368 Anthropogenic structures, such as offshore wind turbines, can attract migratory birds,

369 potentially causing increased mortality through collision (Perrow 2019) or evoke

370 avoidance behaviour leading to increased, delayed, fitness costs due to longer 371 routes and higher energy expenditure (Schwemmer et al. 2023). Such impacts are 372 still largely unquantified on migratory populations of birds (Margues et al. 2021). One 373 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-374 and offshore infrastructure, and contextualise these known individuals amongst con-375 376 and allospecifics, detected by the acoustic recorders (Loring et al. 2019, Willmott et al. 2023). 377

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-384 migratory birds to bright, often urban, areas (McLaren et al. 2018, Smith et al. 2021, 385 386 Horton et al. 2023). These areas may act as potential ecological traps (i.e., 387 inadequate stopover sites that might present higher risk of mortality; Van Doren et al. 388 2021). Similarly, anthropogenic electromagnetic radiation ('electrosmog') has been shown to disrupt the magnetic compass of night-migratory songbirds (Engels et al. 389 2014). As this was observed in the lab environments with caged birds, it poses the 390 question whether 'electrosmog' is also a hazard for freely moving birds in the wild. 391 392 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 393 394 high urban density.

395 <u>Combining Motus tracking with physical samples</u>

Simultaneously collecting samples (e.g. feathers, saliva, blood or faeces) that 396 tell us something about the physiological state of the animals, together with 397 movement behaviour, can help us better understand how the physiology of an 398 399 individual influences its migratory decisions. The high temporal resolution of tracking 400 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). 401 This could for example include site quality, by correlating stopover duration and 402 403 habitat use, as recorded by Motus, with body condition and immune function 404 (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 405 for stopover required by migrants. If not, targeted conservation measures could be 406 taken to restore the missing functions. 407

408 Genetic analyses in conjunction with recorded migratory behaviour (direction 409 and routes, which are accessible with the high spatiotemporal accuracy of Motus), 410 could indicate population-specific differences and possible significant regions in the 411 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 412 413 samples could be used to monitor the prevalence of pathogens that can be linked to body condition, population origin and subsequent migration decisions (ideally 414 415 seasonal migration success; Neima et al. 2020, Morales et al. 2022). In the long 416 term, standardised studies of migratory behaviour combined with sampling of tagged 417 individuals could allow predictions of responses to global climate and habitat changes (Saura et al. 2014, Anderson et al. 2019). 418

419 <u>Practical next steps: the logistics of developing Motus for flyway level research</u>

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.

427 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, 428 Griffin et al. 2020). Ideally, such projects fill in geographical gaps based on species 429 ecology and migratory behaviour already garnered from other technologies (e.g. 430 431 geolocators; Bayly et al. 2018, or radar; Robinson 2023). As well as capital, the 432 development of the network will require significant time and focus to maintain 433 equipment and retrieve data, particularly in remote areas. Such receivers are less likely to be monitored remotely because of signal and power restrictions, and 434 435 therefore greater logistical efforts are required to obtain the stored data and 436 undertake maintenance.

437 Cost per receiver can be realised for as little as $\in 3000 - 5000$ (~ four 438 directional antennas, Sensorgnome receiver), but may approach $\in 10000$ dependent 439 on requirements for installation and precise configuration of antennas. Each tag, 440 whether from CTT or Lotek, is approximately $\in 200$, although this approaches $\in 300$ 441 for the very smallest models. While cheaper than large, satellite enabled tags, this 442 does not approach the low cost of metal or colour rings that allow researchers to 443 capture and mark many thousands of birds. Cost reduction is hampered by limited

444 market competition and a lack of open-source development, which contrasts the
445 collaborative nature of Motus entirely, and must be addressed going forward to allow
446 tagging on a much larger scale.

Lastly, the amount of data collected from Motus is enormous and is likely to 447 continue to grow alongside other biologging data (López-López 2016), so 448 449 appropriate statistical tools will need to continue to be developed. Complex Bayesian modelling frameworks to appropriately analyse Motus data have been developed, 450 and tested in limited circumstances, e.g., modelling movement offshore (Cranmer et 451 al. 2017; Baldwin et al. 2018), and estimating flight heights (Lagerveld et al. In 452 press). Extending the applicability of these methods and developing integrated 453 frameworks with multiple data types would enable researchers to make better use 454 and further inferences about migratory parameters that can inform conservation 455 (Gregory et al. 2023). 456

457 These challenges can only be solved in the long term, with a coordinated, international, collaborative effort, to develop joint funding applications and to work 458 together for the benefit of the wider Motus community. This community must contain 459 academics, policymakers, government officials, conservationists, amateur biologists 460 461 and ecologists, who can develop well-defined, focused study objectives. The 462 involvement of a diverse number of stakeholders is required, not just to share the 463 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 464 465 2020, Gregory et al. 2023; Guilherme et al. 2023).

466 Final Outlook

467 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 468 469 about how species are confronting environmental changes. Motus can provide multi-470 scale data on the movements of bird without the need for recapture, even on species 471 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), 472 and large insects, such as the monarch butterfly (Knight et al. 2019, Wilcox et al. 473 2021). Motus' features and capabilities make it an attractive and exciting prospect for 474 475 exploring as yet unanswered ecological, evolutionary, and behavioural guestions.

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



917 Figure 2: Capability and context of tags enabled for Motus. Icons indicate tag types and are positioned

918 approximately in relation to their mean battery lifetime and size. Grey dotted lines represent variation on both

919 axes taking into account programming influence on battery life and differences among and between device types.

920 Orange 'wifi' symbols represent transmission capability, independent of the bird's return to a specific location.



922 Figure 3a. European Robin (*Erithacus rubecula*) with attached radio transmitter with radio transmitter and

923 attached leg-loop harness illustratively shown above the bird; b. a Motus receiving station (6 metre height), with 4

924 six-element-Yagi antennas pointing in four directions. The station is powered by solar, with a buffer battery (in

925 aluminium box on ground). The electronics are installed in the small yellow box at the pole. Detailed information

926 about tagging animals and building stations can be found at the Motus Webpage (motus.org/resources/) and from

927 the regional Motus coordinators (motus.org/groups/regional-coordination-groups/). Photos: T.K.



929 Figure 4: Current Motus receiving station network (purple dots) across the European

930 continent, along with hypothetical future stations (yellow dots) to demonstrate potential to answer

931 demographic and conservation-focused questions about bird migration. Blue arrows highlight flyways

932 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.