Optimising the use of bio-loggers for movement ecology research

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38   **Abstract**

39   1. The paradigm-changing opportunities of bio-logging sensors for ecological research,

40   especially movement ecology, are vast, but the crucial questions of how best to match

41   the most appropriate sensors and sensor combinations to specific biological questions,

42   and how to analyse complex bio-logging data, are mostly ignored.

43   2. Here, we fill this gap by reviewing how to optimise the use of bio-logging techniques

44   to answer questions in movement ecology and synthesise this into an Integrated Bio-

45   logging Framework (IBF).

46   3. We highlight that multi-sensor approaches are a new frontier in bio-logging, whilst

47   identifying current limitations and avenues for future development in sensor

48   technology.

49   4. We focus on the importance of efficient data exploration, and more advanced multi-

50   dimensional visualisation methods, combined with appropriate archiving and sharing

51   approaches, to tackle the big data issues presented by bio-logging. We also discuss the

52   challenges and opportunities in matching the peculiarities of specific sensor data to

53   the statistical models used, highlighting at the same time the large advances which

54   will be required in the latter to properly analyse bio-logging data.

55   5. Taking advantage of the bio-logging revolution will require a large improvement in

56   the theoretical and mathematical foundations of movement ecology, to include the

57   rich set of high-frequency multivariate data, which greatly expand the fundamentally

58   limited and coarse data that could be collected using location-only technology such as

59   GPS. Equally important will be the establishment of multi-disciplinary collaborations

60   to catalyse the opportunities offered by current and future bio-logging technology. If

61   this is achieved, clear potential exists for developing a vastly improved mechanistic

62   understanding of animal movements and their roles in ecological processes, and for

63   building realistic predictive models.

64

68

Introduction

70

71 Movement is a fundamental aspect of life, intrinsically linked to almost every ecological and

72 evolutionary process, from the acquisition of food, through reproduction and survival, to

73 species distributions and community structure. Decades of technological developments have

74 created vast possibilities in terms of data collection to study the movement of organisms,

75 from VHF (Kenward, 2001), ARGOS and GPS technology (Kays, Crofoot, Jetz, & Wikelski,

76 2015; Tomkiewicz, Fuller, Kie, & Bates, 2010; Weimerskirch, 2009), to reverse GPS

77 technology (Weiser et al., 2016) and dedicated satellite systems for tracking animals around

78 the globe (ICARUS, see Wikelski et al., 2007), to sensor and acoustic receiver networks for

79 animal tracking (Duda et al., 2018; Hoenner et al., 2018). In tandem, ecologists have driven a

80 revolution in bio-logging sensor technology, motivated by the need to gather behavioural and

81 ecological data that cannot be obtained through direct observation. This revolution has

82 resulted in the development and use of a variety of sensors to observe the unobservable,

83 including *inter alia*: accelerometers, magnetic field sensors, gyrometers, temperature and

84 salinity sensors, further complemented by video cameras and proximity-loggers (Rutz &

85 Hays, 2009) - see SI Table 1. The combined use of multiple sensors can provide indices of

86 internal 'state' and behaviour, reveal intraspecific interactions, reconstruct fine-scale

87 movements and even measure local environmental conditions (Rutz & Hays, 2009; Wilson et

88 al., 2014). However, with increasing sensor possibilities comes a new challenge: pinpointing

89 the appropriate information to collect, and finding efficient ways to do so.

90

91 It is hardly surprising, therefore, that there is an increasing number of high-profile reviews

92 that showcase the paradigm-changing opportunities offered by animal-attached technology

93 for ecological research (Hussey et al., 2015; Kays et al., 2015; Wilmers et al., 2015). Within

94 these reviews, however, there exists scant treatment of how best to match the most

95 appropriate sensors and sensor combinations to specific biological questions. As a result,

96 ecologists have tended to use statistical methods *post hoc* to overcome the limitations of

97 specific sensor data, including smoothing methods such as Kalman filtering and state-space

98 models or machine-learning approaches applied to positional and accelerometer data.

99 Similarly, although new analytical methods show great promise, such as the use of machine-

100 learning to identify behaviours from tri-axial acceleration data (Nathan et al., 2012) or

101 Hidden Markov Models (HMMs) to infer hidden behavioural states (Leos-Barajas et al.,

102   2017), no clear guide exists to promote best practices. Such a guide would allow ecologists

103   and statisticians to strike a balance between overly simplistic and complex models to deal

104   with the vagaries of specific sensor data, for example the limitations of accelerometer data

105   (see also Patterson et al., 2017). We aim to fill this gap by considering how to optimise the

106   use of bio-logging techniques to answer key questions in movement ecology. In doing so, we

107   identify four critical areas – questions, sensors, data, and analysis – and related opportunities

108   for multi-disciplinary collaborations, and synthesise these into an Integrated Bio-logging

109   Framework (IBF) to aid the decision-making process for ecologists. We then review the

110   technologies and methodologies available to ecologists to make the links between nodes of

111   the framework. We first consider how best to address biological questions using the most

112   appropriate sensors while identifying current technological limitations. Second, we review

113   the challenges and opportunities of linking new data types obtained from bio-logging sensors

114   to the most adequate analytical techniques. We discuss issues relating to dealing with large,

115   complex datasets, the fundamental properties of the new data types that can be collected, and

116   the challenges of archiving and sharing bio-logging data. Finally, we discuss the value of

117   multi-disciplinary collaborative links to optimise the opportunities offered by current and

118   future bio-logging technology.

119

120   The Integrated Bio-logging Framework

121   We connect the four areas critical for optimal study design via three-nodes in a cycle of

122   feedback loops (Figure 1), linked by multi-disciplinary collaboration. Ecologists can work

123   their way through the IBF to develop their study design – typically, this will start with the

124   biological question, but the pathways will differ if, for example, using a question/hypothesis

125   driven (blue) or data-driven (orange) approach. Figures 2 and 3 provide two such pathway

126   examples.

127

128   Furthermore, bio-logging has become so multifaceted and complex that no-one can be a

129   'master of all trades', hence, establishing multi-disciplinary collaborations is key (as for other

130   disciplines, Peters et al., 2018), and this idea is at the basis of the IBF. For example, at the

131   study inception phase, dependent on the biological problem addressed, physicists and

132   engineers can advise on sensor types, their limitations and power requirements, while

133   mathematical ecologists and statisticians can aid in framing the study design and modelling

134   requirements for specific questions (see Figure 2). Development of bio-logging tags is the

135   result of collaborations between engineers, physicists and biologists, while visualisation and

136   analytical methods for dealing with data are aided by interactions with computer scientists,

137   geographers, statisticians and mathematicians (see Figure 3). On the other hand, ecologists

138   can guide researchers from the other disciplines towards the key methodological hurdles and

139   technological limitations which are hindering progress and need to be addressed.

140

141   We now review the literature regarding questions, sensors, data and analyses, and exemplify

142   the links between the nodes of the IBF. We conclude by highlighting areas for future

143   development.

144

145   **1. From questions to sensors**

146   Researchers can choose between an ever-increasing number of different bio-logging sensors

147   (Table 1, SI Table 1). Following the adage that experimental design should be guided by the

148   questions asked (e.g. Fieberg & Börger, 2012; Hebblewhite & Haydon, 2010), sensor choice

149   is clearly critical. Here, we consider sensor selection within the general scheme of key

150   movement ecology questions posed by Nathan et al. (2008) and provide an example for the

151   use of the IBF in a question-driven approach to study design (Figure 2).

152

153   *1.1 Where is the animal going?*

154   ARGOS, GPS and related satellite and global navigation systems, as well as acoustic tracking

155   arrays and geolocators, have revolutionised information on animal locations and movements

156   (Kays et al., 2015). Bio-logging sensors, particularly in combination with such locational

157   tracking-devices, can further help detect where animals move. For example, Hedenstrom et

158   al. (2016) combined geolocator and accelerometer tags to record flight behaviour of

159   migrating swifts, and Shipley, Kapoor, Dreelin, & Winkler (2018) used micro barometric

160   pressure (altitude) sensors (<0.5 g) to uncover the aerial movements of migrating birds. A

161   key limitation of telemetry devices is that transmission technology can fail, such as when

162   canopy cover impedes GPS satellite fixes (Rempel, Rodgers, & Abraham, 1995). However,

163   with the combined use of inertial measurement units (IMUs) and elevation/depth recording

164   sensors it is possible to reconstruct animal movements in 2D and 3D using a dead-reckoning

165   procedure, irrespective of transmission conditions (Bidder et al., 2015; Bramanti &

166   Dall'Antonia, 1988). This uses the speed (including speed-dependent dynamic body

167   acceleration (DBA) for terrestrial animals; Bidder, Qasem, & Wilson, 2012), combined with

168   animal heading (from magnetometer data) and change in altitude/depth (pressure data) to

169   calculate the successive movement vectors (oriented steps) from a known starting position.

170 The process gives extraordinarily finely resolved relative movement (it can, for example,

171 determine how many times a dog has walked around a tree in scent-marking activity) but it

172 can accumulate errors over time, especially in fluid media with current flow. Therefore, data

173 used in dead-reckoning need correcting with frequent ground-truthing, such as by a GPS unit

174 (Bidder et al., 2015). GPS-enabled dead-reckoning is an incredibly powerful combination of

175 sensor systems which may become paradigm-shifting within animal movement studies. With

176 this, researchers will have access to multiple scales of movement and seamless animal

177 movement descriptors and will be able to identify true turn-points in the data (Potts et al.,

178 2018; see Figure 2 and section 3.3 below). In turn, the improved track trajectory should allow

179 us to connect behaviour to landscape ecology and population dynamics with increased

180 confidence (Morales et al., 2010).

181

182 *1.2 How is the animal moving?*

183 At the smallest scale (locomotion), animals move according to their anatomy and the

184 biomechanics that this engenders, with obvious differences between animals operating in

185 fluid media (air or water) or on the ground (Biewener & Patek, 2018). In essence, locomotion

186 is manifested by particular patterns of movement by the various body parts (most notably

187 limbs) so that motion-sensitive transducers can provide critical information with respect to

188 the pattern and intensity of movements and thereby derive critical whole-animal movement

189 parameters such as speed and direction. The primary sensors used for this include

190 accelerometers, magnetometers and gyrometers (often collectively grouped within inertial

191 measurement units [IMUs]; e.g. Noda, Kawabata, Arai, Mitamura, & Watanabe, 2014).

192 Accelerometers and magnetometers can be used to infer the 3D posture and orientation (i.e.

193 azimuth, elevation angle and bank angles; see SI Table 1 for a glossary of terms) during

194 locomotion, whereas gyrometers provide direct measures of yaw, pitch and roll (see

195 Benhamou, 2018 for the mathematical relationships between these parameters). In addition,

196 various iterations of speed-detecting systems, such as anteriorly mounted propellers (Ropert-

197 Coudert et al., 2000; Watanabe et al., 2008), flexible paddles (Shepard, Wilson, Liebsch, et

198 al., 2008), and Pitot tubes are also used (Taylor, Reynolds, & Thomas, 2016). Importantly,

199 the speed at which an animal is moving provides information on the urgency with which the

200 movement is being undertaken. When moving animals deviate from minimum cost of

201 transport (cf. Schmidt-Nielsen, 1972), it indicates time-based selection pressures that incite

202 animals to move non-optimally in energetic terms; the reasons for which may be critical for

203 lifetime fitness and only become apparent *post hoc* (e.g. Shepard, Wilson, Quintana, Laich, &

204   Forman, 2009). Sensors are thus required to record information from which we can quantify

205   the energetics of animal locomotion, as well as the costs and benefits of behaviours. Several

206   sensors provide proxies for oxygen consumption (VO_2), including heart rate loggers (Green,

207   2011) and tri-axial accelerometers through the computation of dynamic body acceleration

208   (DBA; reviewed in Wilson et al., 2019). Indeed, the continued refinement of these proxies of

209   power use, one of the most fundamental currencies in the animal kingdom, will be pivotal in

210   providing critical, missing information within previously established movement frameworks

211   such as optimal foraging (McNamara & Houston, 1986; Pyke, 1984).

212

213   Sensors that detect body movements may also provide key information relating to

214   biomechanical questions, such as how stroke frequency relates to stroke amplitude. For

215   example, magnets used with Hall sensors (sensors detecting magnet-transducer paired

216   magnetic field properties; Hall, 1879 - see S1 Table 1) can quantify the amplitude, angular

217   velocity and frequency of limb movements of marine mammals (Wilson & Liebsch, 2003),

218   providing insights into energy-saving mechanisms (Nassar, Jackson, & Carrier, 2001).

219   Animal-borne video or audio may provide similar information, for example, being able to

220   relate flipper beat frequencies in green turtles (*Chelonia mydas*; Hays, Marshall, & Seminoff,

221   2007) and emperor penguins (*Aptenodytes forsteri*; van Dam, Ponganis, Ponganis, Levenson,

222   & Marshall, 2002), to dive strategies. Hall sensors can also measure respiration rates and

223   extent of inhalation, heart rates, and even patterns of defaecation, providing information on

224   the optimal breathing strategies and rates of digestion (Wilson et al., 2003, 2004), cases

225   where mounted-accelerometers would be limited due to movement being mainly

226   translocational. In addition, these behaviours can also be detected from on-board videos. Yet

227   few studies use these techniques, perhaps because researchers find the magnetic field

228   intensity drop off with distance intractable and because, at the time the studies were

229   published, it was not possible to study angular changes between magnet and sensor, if

230   distances were held constant. Inertial measurement units (IMUs) have changed this, so we

231   think that the future of miniature IMUs holds promise for researchers to document minute

232   changes in body movement and for quantifying motion capacity from limb movements.

233

234   *1.3 What is the animal doing?*

235   Allocating behaviours to space is key to understanding animal niche requirements and the

236   link between behaviour and fitness consequences. Since the work by Yoda et al. (1999) using

237   accelerometers to determine animal behaviour, there is a rich and varied literature that

238 documents increasingly successful methodologies for determining animal behaviour from
239 various sensor data, especially accelerometers (Nathan et al., 2012; Shepard, Wilson,
240 Quintana, et al., 2008) and magnetometers (Williams et al., 2017). Thus, it is now possible to
241 extract a remarkable amount of information regarding behaviour, beyond that of limb and
242 body part movement as detected from tri-axial sensors.

243

244 In particular, quantifying the type and amount of food ingested by animals is essential to
245 answering some of the "big questions" in movement ecology such as how animals manage
246 their energy budgets in the wild (cf. Krebs & Davies, 1978). For example, combining GPS
247 and DBA measures derived from tri-axial accelerometers, allows us to better understand the
248 energetics underlying prey capture behaviour of large terrestrial predators (Wilmers, Isbell,
249 Suraci, & Williams, 2017), while the drift and buoyancy inferred from time-depth recorders
250 can provide information on the foraging success of marine predators (Abrahms et al., 2018).
251 A further refinement is provided by indirect parameters such as those obtained by means of
252 sensors that detect stomach, oesophageal or visceral temperature, which can provide
253 invaluable insights into actual prey captures (Weimerskirch, Gault, & Cherel, 2005;
254 Weimerskirch, Pinaud, Pawlowski, & Bost, 2007; Wilson, Cooper, & Plötz, 1992). An
255 intriguing alternative is based on attaching a Hall sensor to one mandible opposite a magnet
256 attached on the other mandible (but the ethical implications and feasibility must be well
257 considered). The inter-mandibular angle can be determined by measuring changes in
258 magnetic field strength (Wilson, Steinfurth, Ropert-Coudert, Kato, & Murita, 2002). This
259 approach, which has been employed in several marine and terrestrial species, can provide
260 information about both the number of food items and the type of food ingested (Ropert-
261 Coudert et al., 2004). Indeed, such is the detail provided by these sensors that studies are now
262 able to examine food acquisition within a probabilistic framework and thereby make
263 predictions about how food abundance may affect populations (Wilson, Neate, et al., 2018).

264

265 Obtaining direct observations may sometimes be essential, either because robust calibration
266 of bio-logging sensors is difficult, or because the study's aim is to document particular
267 behaviours in great detail (such as prey captures and social interactions; McInnes, McGeorge,
268 Ginsberg, Pichegru, & Pistorius, 2017; Pagano et al., 2018; Watanabe & Takahashi, 2013) or
269 to prospect for undiscovered behaviours (such as unusual foraging techniques; Rutz, Bluff,
270 Weir, & Kacelnik, 2007). Under these circumstances, video loggers are the method of choice,
271 or still-image loggers, if longer recording times are required and a lower frame rate is

272 acceptable. Cameras may also offer the opportunity to assess what a wild animal sees in the

273 field (Moll, Millspaugh, Beringer, Sartwell, & He, 2007) so that environmental information

274 can be factored into foraging efficiency (Sutton, Hoskins, & Arnould, 2015) and movement

275 patterns studied with respect to visual stimuli (Tremblay, Thibault, Mullers, & Pistorius,

276 2014). Video loggers can also be combined effectively with other sensors such as

277 accelerometers (Watanabe & Takahashi, 2013), and are small enough to be fitted to a wide

278 range of species (see below).

279

280 *1.4 Why is the animal moving?*

281 Animals make behavioural decisions based on their internal 'state' (physiological and

282 psychological condition), and external biotic and abiotic factors (Nathan et al., 2008).

283 Identifying and quantifying how internal state may drive behaviour is non-trivial, and can

284 often only be indirectly inferred (Getz & Saltz, 2008). Some aspects of animals' internal state

285 have been investigated using accelerometers which are sensitive to micro-movements and

286 postures indicative of chemical, disease, and affective states (Downey et al., 2017; Wilson et

287 al., 2014), including vigilance behaviour, a stress-related response (Kröschel, Reineking,

288 Werwie, Wildi, & Storch, 2017). Alongside accelerometers, other key sensors that can

289 provide insights into internal state include heart rate, internal temperature, and neurological

290 sensors (Rattenborg et al., 2016). For example, heart rate loggers to investigate the interplay

291 between ecological pressures and energetic strategies were used by Bishop et al. (2015) in

292 bar-headed geese (*Anser indicus*) and O'Mara et al. (2017) in fruit-eating bats (*Uroderma*

293 *bilobatum*). As another example, Ditmer et al. (2018) used heart rate loggers to investigate

294 how American black bears (*Ursus americanus*) perceive the risks of crossing roads. Research

295 on humans has demonstrated that bio-loggers can measure a suite of physiological variables

296 relating to internal state (Nikita, 2014; Yang, 2014) and the development of similar systems

297 for wild animals is increasing; examples include animal-borne blood sample collection

298 devices for stress hormones in seals (Takei et al., 2016), other hormonal sensors (Landry et

299 al., 2014), and internal chemical detection nanosensors for freely moving animals (Lee et al.,

300 2018) .

301

302 The greatest insight into state-driven movement is likely to be gained from multi-sensor

303 approaches (e.g. Wilson, Littman, Halpin, & Read, 2017), especially combining both

304 physiological and/or neurological sensors with position-determining systems (Figure 2). For

305 example, Vyssotski et al. (2006) simultaneously measured pigeon (*Columba livia*) movement

9

306 and electrical brain activity using a miniaturised GPS combined with an
307 electroencephalography logger, while Dunn et al. (2016) obtained a brain-wide mapping of
308 neural activity of zebrafish (*Danio rerio*) during movement. The use of neurological sensors
309 to monitor brain activity in freely moving animals is a relatively new advancement (e.g.
310 Rattenborg et al., 2016; Skocek et al., 2018). Such multi-sensor developments are helping to
311 meet the challenge of linking internal state, as a proximate cause of movement, to ultimate
312 evolutionary causes (Nathan et al., 2008). However, there are important ethical
313 considerations to be raised, especially for surgically implanted sensors (e.g. the example of
314 frigatebirds, Rattenborg et al., 2016).

315

316 Alongside the internal state, what is happening in the environment is the other prime driver of
317 animal movement. Global environmental data can be recorded through satellite remote
318 sensing, and bio-loggers now routinely collect local environmental data both biotic and
319 abiotic (Table 1; SI Table 1), thus a major aspiration is to link such data to movement.
320 Though whilst ecologists can access an increasing amount of remote-sensed environmental
321 data, linking them to location data is usually difficult, as environmental data are obtained at
322 different, generally coarser, spatiotemporal scales than movement data (Dodge et al., 2013).
323 Remelgado et al. (2019) recently developed a new pixel-based approach, combined with data
324 mining and visualisation, to help ecologists efficiently deal with differences in the spatial,
325 temporal and thematic resolutions between environmental data from remote sensing and GPS
326 location data; yet the problem persists with high frequency bio-logging data.

327

328 Depending on the question asked, it may be necessary to use modelling to derive high-
329 accuracy dynamic maps of environmental conditions (e.g. vertical wind; see Scacco, Flack,
330 Duriez, Wikelski, & Safi, 2019), or to use drones or LiDAR, to build ultra-high resolution, 2-
331 and 3-dimensional maps of the study area (e.g. to investigate movement costs due to
332 elevation or to quantify vegetation quality for optimal foraging questions). Importantly, bio-
333 loggers allow the collection of high-frequency environmental data at the local scale
334 experienced by the animals, such as temperature, light intensity, and wind or current velocity
335 (Block, 2005; Dodge et al., 2013; Piersma & Lindström, 2004). This may be complemented
336 by implanted sensors such as core body temperature sensors (e.g. when studying heat stress
337 questions), combined with sophisticated use of meteorological data to estimate the so-called
338 wet bulb globe temperature index (WBGT), a key measure of heat stress (Dimiceli, Piltz, &
339 Amburn, 2011).

340

341 In terms of the biotic environment', an animal's movement decisions are likely to be

342 influenced by interactions with conspecifics and heterospecifics and again, there are certain

343 combinations of sensors that can record and help identify these interactions. There are two

344 main approaches to remotely record the social contact between free-ranging animals: indirect

345 and direct encounter mapping (see Bettaney, James, St Clair, & Rutz, 2015; Krause et al.,

346 2013). Indirect encounter mapping can be achieved either with high-resolution tracking of

347 subjects, or with the use of tags that transmit to, or that are detected by, fixed receiver

348 stations at specific locations (e.g., coded VHF radio-tags or PIT/RFID tags). In both cases,

349 the co-occurrence of animals is inferred at the data analysis stage. Direct encounter mapping,

350 on the other hand, requires the use of proximity loggers (transceiver tags that both transmit

351 and receive radio signals between animals) or camera tags (Hooker, Barychka, Jessopp, &

352 Staniland, 2015), to create reciprocal records of social encounters (Bettaney et al., 2015;

353 Krause et al., 2013). Proximity-loggers can be used for addressing a variety of biological

354 questions, and have the advantage over cameras (e.g. Takahashi et al., 2004) that they survey

355 in all directions (even though precise directional and distance information is often not

356 collected), but their key strength lies in charting social associations of a large number of

357 subjects of known identity, to reconstruct group, community, or even population-level social

358 networks. Proximity sensors can also be used to record interspecific encounters, for example

359 between predators and their prey, between different disease hosts, or in mixed groups of

360 foraging or migrating animals. Some systems are set up as wireless sensor networks where

361 animal-mounted sensors not only communicate with other sensors, but also with (a large

362 number of) stationary receiver (base) stations (Rutz et al., 2012). This enables near real-time

363 data transmission, which is key to evaluating system performance and to planning and

364 monitoring experimental manipulations (St Clair et al., 2015).

365

366 A particular type of interspecific interaction occurs when animals interact with human

367 activities, which can strongly affect animal movements (e.g. Tucker et al., 2018). An

368 interesting development is animal-borne radar detectors, which detect signals from emitting

369 radars in the surroundings and can be used in combination with a tracking device to log the

370 occurrence of structures along an animal's movement path (Table 1; SI Table 1). This has

371 facilitated the study of seabird-fishing vessel interactions, quantifying attraction, attendance

372 and foraging behaviour (Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018).

373

374　**2. From sensors to data**

375　Data collection and analysis issues must be addressed alongside sensor selection when

376　approaching a specific ecological question. The first challenge concerns finding the most

377　appropriate experimental/sampling design to answer a given ecological question. More

378　broadly (see the internal data node of the IBF), this concerns the closely related issues of tag

379　design and data management (which includes planning for data archiving and sharing) – all

380　of which must be defined prior to tag deployment. The experimental design will strongly

381　benefit from interdisciplinary collaborations to find the best solution, ensuring that the data-

382　gathering is both feasible and will lead to sufficient data to answer the questions using

383　available analytic techniques.

384

385　*2.1 Experimental design*

386　Consideration of an appropriate sampling regime prior to tag deployment, so as not to over-,

387　or under-sample and maximise battery duration (and minimise tag weight), is a crucial aspect

388　(note that battery power is required both to interrogate the sensors and write the data to

389　memory, and possibly send the data). To do so, researchers should apply the Nyquist or

390　sampling theorem, which states that the sampling frequency should be at least twice the

391　fastest frequency of interest; e.g. consider wingbeat frequency vs. amplitude as focus of

392　interest. This holds true in temporal and spatial domains (see discussion in Ropert-Coudert &

393　Wilson, 2004). An obvious consequence of this trade-off is the use of smart sampling,

394　whereby the sensors record at a frequency able to elucidate the relevant aspect properly, but

395　no more. We do note, however, that highly prescribed, low frequency sampling may miss

396　serendipitous observations of importance and may preclude the detection of new, never

397　observed behaviours. Furthermore, derivation of body motion or measures of energy

398　expenditure (DBA) requires smoothing of accelerometer data at an appropriate frequency

399　(Shepard, Wilson, Halsey, et al., 2008), albeit the latter could indeed be processed on-board

400　without storing the high frequency data (e.g. Cox et al., 2018). For example, a high frequency

401　recording of raw data (> 20 Hz) may be necessary to compute animal posture and DBA (see

402　also Brownscombe, Lennox, Danylchuk, & Cooke, 2018); however, higher frequencies draw

403　more current (doubling the frequency from 20 Hz to 40 Hz might require to double or more

404　the battery size/capacity, and hence weight, depending on the specifics of the sensors), thus a

405　balance between behaviour resolution, information gain, and current draw is a key stage of

406　experimental design. Equally important, when using IMUs featuring multiple sensors, might

407　be to set different frequencies for different sensors, such as a higher frequency for

408   accelerometers (40 Hz), a lower frequency for magnetometers (20 Hz), and an even lower

409   frequency for temperature or pressure sensors (e.g. 4 Hz). Such settings can more than double

410   the time a logger can record on a given battery size (note also that differences between

411   battery types in the capacity to respond to peak current demands from the sensors can further

412   affect the longevity of loggers), but preliminary studies for different study species, and

413   interactions with engineers, might be required to find the best settings. Another area of

414   current research (e.g. see Cox et al., 2018) is focussing on finding clever ways to store on-

415   board only sub-sampled or summary data, rather than the raw high-frequency data, thereby

416   reducing data storage requirements and, ideally, allow remote transmission of the data (often

417   the latter is precluded for field studies due to the high power requirement). Closely related is

418   the choice of sensor resolution (bit resolution, see discussion and examples in Ropert-Coudert

419   & Wilson, 2004). The number of bits with which the data are stored directly determines the

420   quality of the data obtained. For example, past loggers used an 8-bit resolution, meaning the

421   sensor can obtain an absolute resolution given by the maximum resolution range divided by

422   256. In the case of a depth pressure transducer with a maximum range of 50 Bar this means a

423   maximum resolution of circa 0.2 Bar, equal to resolving dive differences of 2 m (a 16-bit

424   resolution allows instead to resolve steps of 0.008 m, see Ropert-Coudert & Wilson, 2004).

425   Low resolution may preclude recording key information such as prey capture events. Equally

426   important is the measurement range of the sensor. For example, an accelerometer which

427   records up to 8 *g* will miss any data of animals moving more dynamically (e.g. head impacts)

428   and unless the animals are known to be only relatively slow moving and good preliminary

429   data exist, researchers should set the range to at least 16 *g* for initial studies (for terrestrial

430   systems; a lower range may be sufficient for aquatic systems as, due to friction, movement

431   speed may change less fast), and record this information in the metadata. Equally important

432   are trade-offs between the quantity of data collected and the time a tag collects data on an

433   individual, as well as trade-offs between the amount of data collected on single individuals

434   against the number of different animals monitored across time and space (see also

435   Hebblewhite & Haydon, 2010). Collaborations across disciplines are crucial to make such

436   decisions.

437

438   2.2 *Tag design*

439   Reducing battery consumption not only extends the life of a bio-logging device, but has

440   implications for tag size and attachment that should also be considered for both optimal study

441   design and animal welfare. Reduction of tag size is paramount, yet even with recent advances

442   in the reduction of sensor size, it is still battery size that limits that of the device. Note also

443   that further evidence demonstrates that for some applications the total mass of the tag

444   together with the animal is more important than the relative tag mass (Tomotani et al 2019).

445   For cameras for example, current available loggers are small enough, at approximately 10 g,

446   to be fitted to a wide range of species (Rutz et al., 2007). However, even state-of-the-art

447   camera loggers remain severely battery limited, hence duty cycling is advisable for most

448   applications, as this allows targeted data collection during periods of peak activity and/or

449   repeated short-term recording over the course of several days (Rutz & Troscianko, 2013). An

450   exciting recent development is the use of event-triggering technology that allows cameras to

451   be switched on whenever particular behavioural states or environmental conditions are

452   detected (see analysis section below). To provide an example, whilst miniature VHF tags

453   weighing 0.5g may allow to track the movements of an animal for up to a month, a battery

454   one or two orders of magnitude heavier would be required to record high-frequency

455   accelerometer and magnetometer data for the same duration. On the other hand, a GPS

456   running at 1 Hz may require between 30-50 mA of current, where as a modern IMU

457   recording tri-axial acceleration and magnetometer data at 40 Hz requires only 5-10 mA of

458   current (Bidder et al. 2014). More generally, close attention in required on how size,

459   longevity, and attachment differ among different tags/sensors. Body et al (2017) provide a

460   useful key for assessing device impacts prior to tag deployment, and a growing body of

461   literature now highlights the importance of tag shape and attachment in terms of affecting an

462   animals drag in aerial and marine environments (e.g. Kay et al 2019, Lear et al 2018,

463   Vandenabeele et al. 2014).

464

465   *2.3 Data management*

466   A further consideration for optimal experimental design is that of data management and

467   processing. The data provided by sensors often do not correspond directly to the information

468   we look for, but to a proxy, which needs to be converted. For instance, a depth recorder is

469   designed to provide a measure of pressure rather than a measure of depth, but underwater

470   depth being linearly related to pressure, the conversion is straightforward. For other sensors,

471   this is not so obvious, and raw data therefore require being pre-processed. For example,

472   acceleration data do not provide a direct estimate of energy expenditure or oxygen consumed

473   while moving. First, the dynamic component has to be extracted from the raw acceleration

474   values, then converted to DBA, which finally has to be correlated with energy or oxygen

475   through controlled lab experiments (reviewed in Wilson et al., 2019). Pre-processing is also

14

476   required for integrating data provided by different sensors, possibly at different rates, and
477   often based on separate clocks (exposing systems to clock drift); although inertial
478   measurement units (IMUs) effectively deal with temporal synchronisation within any one
479   logger. Notably, data recorded at high frequency are both noisy and highly serially auto-
480   correlated. Noise can be reduced by filtering, e.g. by taking a running mean, or may involve
481   more complex approaches such as Fourier transformations or Kalman filtering (e.g. Alam &
482   Rohac, 2015). A simple and efficient solution consists of sub-sampling the processed data to
483   a level (or deriving averages) to accord with the Nyquist frequency. Pre-processing should be
484   performed before subsampling, although there is an element of feedback depending on the
485   desired end-point, which may also need to be considered when selecting the sampling
486   frequencies for the different sensors and their data types, which also has important
487   implications for data archiving (see next section).

488

489   *2.4. Data archiving and sharing*

490   Bio-logging data also present considerable challenges for data sharing and replicability. One
491   challenge lies in the lack of standardised protocols for data recording from animal-borne
492   sensors (Campbell, Urbano, Davidson, Dettki, & Cagnacci, 2016). Logging data require very
493   detailed metadata on the attachment type and position on the animal of the loggers, as
494   otherwise, establishing a close relationship between the output from sensor data (such as tri-
495   axial accelerometer) and the orientation and posture of the animal, will be near impossible.
496   Furthermore, whether or not to keep both the pre- and post-processed versions of the data
497   (particularly before or after filtering and subsampling) is something to consider in terms of
498   not only the current question and analyses, but also for the long-term goals of archiving data
499   in the best format available to allow long-term use of those data. Thus, there is an urgent need
500   to improve data protocols and database standards for bio-logging data. Indeed, the
501   International Bio-Logging Society is actively working towards that goal. Efficient data
502   sharing and archiving across many studies and authors will be key to answer the big
503   questions in movement ecology, e.g. global responses to environmental change (Figure 3),
504   and will reduce the need to collect new data (see also section 4).

505

506   **3. From data to analysis**

507   Data analysis issues must be addressed upfront alongside sensor selection and experimental
508   design, to ensure the resulting data are sufficient for the proposed mathematical models and
509   statistical tests used to infer biological information from the data. This requires strong inter-

510   disciplinary collaborations between empiricists and theoreticians from the outset of the

511   project. The first major challenge for the link between data collection and analyses in the IBF

512   is the 'big data' problem. Rapid advances in bio-logging technology now provide

513   information-rich, big data sets, even from single individuals, thus the challenges in data

514   analyses are similar to those of 'big data' and 'data science' problems in ecology and other

515   scientific disciplines (Hampton et al., 2013; Lewis, Vander Wal, & Fifield, 2018; Thums et

516   al., 2018). There is an urgent need for the use and development of more sophisticated and

517   computationally efficient data visualisation and exploration methods, as well as mathematical

518   models that incorporate multidimensional bio-logging data.

519

520   *3.1 Data Visualisation*

521   A key part of exploratory data analysis consists in devising efficient ways to visualise and

522   display quantitative information (Tukey, 1977), especially to aid exploration in this data-rich

523   era. Data visualisation converts complex patterns in data into a visual display, capitalising on

524   the extraordinary capacity of the human visual system to pick out patterns in complex

525   landscapes, and thereby provide insights into data relations (Ware, 2012). While ecologists

526   often develop their own visualisation tools, many methods come from other disciplines such

527   as geographic information science (Demšar et al., 2015; Li, Wu, Song, & Zhou, 2016),

528   medicine and neuroscience (with complex fMRI data e.g. de Ridder, Klein, & Kim, 2017).

529

530   Conventionally, acceleration data tend to be visualised as time series plots (Figure 4A), with

531   analyses based on summary statistics (derived from ethograms; Figure 4B) and the

532   application of data transformations. While such approaches are useful for classification of

533   time series data (Walker et al., 2015), integration of multi-sensor data are poorly covered by

534   this approach (Lee & Jeong, 2017; Li et al., 2016; Walker, Borgo, & Jones, 2016), primarily

535   due to time taking up one axis and constraining all other data to lie within its scaling and

536   bounds. Other visualisations may bypass the time scaling factor by having spherical plots that

537   present 3-dimensional scatterplots, histograms, clustering data by behavioural state (Grundy,

538   Jones, Laramee, Wilson, & Shepard, 2009; Williams et al., 2017; Wilson et al., 2016; Figures

539   4C-E). The value in these spherical plots is that they are also multi-layer and present

540   environmental data such as pressure and temperature as well as metrics of energetic

541   expenditure (Roberts, Laramee, & Jones, 2015). In addition, time can also be represented, if

542   necessary, by glyph or line colour (Figure 4E). Thus, such visual analytics systems can be

543   linked interactively to allow different aspects of the same data to be explored, with and

544 without temporal and spatial scales. In terms of sensor data this includes plots in tri-axial

545 space with further dimensions related to movement and performance metrics (e.g. Roberts et

546 al., 2015) and those that combine multi-dimensional trajectory visualisations on a map with

547 environmental data (e.g. Buchin et al., 2015; Shamoun-Baranes et al., 2016; Figure 4F) and

548 temporal visualisations (Demšar et al., 2015) such as DynamoVis (Dodge, Xavier, & Wong,

549 2018; Xavier & Dodge, 2014) and trackplot (Ware, Arsenault, Plumlee & Wiley, 2006) or

550 flow visual analytics systems (Andrienko, Andrienko, Chen, Maciejewski, & Zhao, 2017;

551 Graser, Schmidt, Roth, & Brändle, 2017; Figure 4G). Time is also commonly visualised

552 through animation and there are two R packages that support this (albeit for traditional

553 location-only data, not logger data): moveVis (Schwalb-Willmann, 2018) and anipaths

554 (Scharf, 2018). See supplementary information for a detailed list of current visualisations (SI

555 Table 3). Current developments indicate that it may be possible to bring these multi-

556 dimensional plots into an interactive 3-dimensional lab space beyond a digital screen, which

557 would dramatically help exploration of data and even advance behavioural studies through

558 the manipulation of the virtual world (see Stowers et al., 2017). Equally important will be the

559 development of improved ways to display results from machine-learning methods (see

560 below); again, an area for which multi-disciplinary collaborations will be crucial.

561

562 *3.2 Behavioural Classification*

563 Behavioural classification involves identifying particular behaviour-linked signals within

564 complex datasets, such as accelerometer and magnetometer data. This may involve searching

565 for behaviour-linked thresholds, such as an increase in pressure to indicate diving (Kooyman,

566 1964) but more commonly will involve consideration of multiple data streams (Viviant,

567 Trites, Rosen, Monestiez, & Guinet, 2010; Yoda et al., 2001), which makes the process more

568 complex. For this reason, much emphasis has recently been placed on machine learning

569 algorithms (including K-Nearest Neighbour [KNN], Support Vector Machines [SVMs],

570 Classification and Regression Trees [CART], and Artificial Neural Networks [ANNs]) to

571 classify behaviours automatically (Nathan et al., 2012). Supervised machine-learning models

572 are trained with segments of data that have been manually labelled according to behaviour

573 (Carroll, Slip, Jonsen, & Harcourt, 2014; Watanabe & Takahashi, 2013). The convenience of

574 machine-learning systems is that they require little specialist knowledge and information

575 about the data streams from the researcher. Against this, there is a tendency to put all primary

576 data streams as well as derived elements (such as DBA metrics) into the process. Because the

577 machine does not know which data streams are most relevant at the outset, processing times

578 can be prohibitively long. An approach that attempts to deal with this uses a Boolean

579 framework and requires that the researchers have enough specialist knowledge to be able to

580 pick out a sequence of features in behaviours (systematic variation and direction in data

581 streams over defined time periods) to be able to define the behaviour in a series of key

582 elements. These are then defined in an algorithm and the computer made to search for exactly

583 those conditions to define the behaviour (Wilson, Holton, et al., 2018). The obvious

584 downside to this approach is the level of expertise of the user and familiarity with the

585 meaning of the data streams, which highlights the crucial role ecologists and biologists have

586 to play in making sure analyses remain biologically sound and relevant. On the other hand,

587 bio-logging sensor data allow for the discovery of behaviours never seen before in animals

588 (Wilson et al., 2014), thus both exploratory and confirmatory analyses, as well as supervised

589 and non-supervised data analysis methods will be equally important for ecologists (see also

590 Leos-Barajas et al., 2017). Behaviour classification using logger data can also inform the

591 usage of limited, or previously collected, GPS and track data to identify different behaviours

592 (e.g. Browning et al., 2018).

593

594 *3.3 Movement analyses in the bio-logging era*

595 There is a long history of theoretical investigation into the reasons and rules underpinning

596 animal movement (Nathan et al., 2008) including, for example, optimal foraging theory

597 (Houston, Clark, McNamara, & Mangel, 1988; Pyke, 1984). However, historically, there

598 have been inadequate data on the energetics and the details of movements to embrace

599 optimality properly. Consequently, theoretical movement ecology has tended to focus on

600 statistical descriptions of movement that are agnostic to the underlying life-history needs that

601 govern movement decisions. Step-selection analysis, for example, examines environmental

602 features that are correlated to movements from one location to the next (Avgar, Potts, Lewis,

603 & Boyce, 2016; Fortin et al., 2005; Thurfjell, Ciuti, & Boyce, 2014). As another example,

604 there are a variety of techniques that use movement to infer changes in behaviour, by

605 observing how features such as speed, or tortuosity change over time (Hooten, Johnson,

606 McClintock, & Morales, 2017). These are categorised under various names such as state-

607 space models (Jonsen et al., 2013; Morales, Haydon, Frair, Holsinger, & Fryxell, 2004;

608 Patterson, Thomas, Wilcox, Ovaskainen, & Matthiopoulos, 2008), hidden Markov models

609 (Langrock et al., 2012; McClintock & Michelot, 2018), continuous time models (reviewed in

610 Patterson et al., 2017), and behavioural change-point analyses (Edelhoff, Signer, &

611 Balkenhol, 2016; Gurarie, Andrews, & Laidre, 2009). Similarly, there has been significant

612 interest in inferring broad-scale movement patterns, such as home range, migratory or
613 dispersal patterns, from squared displacement statistics (Börger & Fryxell, 2012). There is
614 also a long history of mathematical models for inferring space-use patterns from general
615 features of movement, such as advective and diffusive components (Moorcroft & Lewis,
616 2006; Moorcroft, Lewis, & Crabtree, 1999; Potts & Lewis, 2014). All of these examples
617 model movement in a descriptive fashion, where the biases and correlations (Benhamou,
618 2014; Codling, Plank, & Benhamou, 2008) represent hypothesised behavioural features of the
619 movement path and the aspects of the movement that we either do not have direct knowledge
620 of or are unable to test, as 'random walks', or 'hidden states'. Incorporating high-resolution
621 information from bio-logging studies can change this, as well as enable us to answer
622 questions that link movement decisions to the life-history needs of animals.

623

624 Step selection analysis (SSA) is one of the most widely-used techniques for inferring the
625 environmental drivers behind observed movement patterns. New bio-logging technologies
626 enable us to build upon SSA in two important ways. First, the ultra-high frequency locations
627 given by dead-reckoned IMU data enable us for the first time to find the precise points at
628 which an animal changes direction (Potts et al., 2018), rather than assuming (implicitly) that
629 changes in direction occur at the points where locations are acquired (which is typical in SSA
630 studies based on GPS data, although there are exceptions; e.g. Merkle, Fortin, & Morales,
631 2014). Second, this approach can be extended to examine broader changes in the state of the
632 animal, rather than simply its location, and without having to recur to statistical models trying
633 to infer a 'hidden state'. As such, we might parametrise a model containing not only the
634 locations of the animal, but also any of the other aforementioned features that we can
635 measure (or infer from metrics of movement) from bio-logging technology, such as head-
636 position, heart-rate, movement "mode" (running/eating) or even interaction variables related
637 to the movement of others in the environment (SI Box 1).

638

639 For example, by modifying step selection analysis and similar techniques to incorporate the
640 energetic costs and benefits derived from detailed bio-logging data (acceleration and heart
641 rate loggers), we may be able to uncover the bio-energetic reasons behind animal movement
642 choices, rather than simply describing landscape aspects that co-vary with animal movement.
643 This would help us re-visit old questions about the optimality of foraging decisions, and give
644 important behavioural insights into animal decision-making at fine scales as they move
645 through their energy landscape (Shepard et al., 2013). Quantifying the effects of the

646 environment on movement costs in this way could help also derive a proxy of energy cost
647 based on environmental conditions, to use with movement data without bio-logging
648 information (e.g. Figure 3).
649
650 An interesting development in that direction is by Hooten, Scharf, & Morales (2018), who
651 present a new approach to analyse movement data, including explicit mechanistic links to
652 physiological dynamics, to better model decision making and movement in heterogeneous
653 environments. Notably, this approach can be extended to accommodate additional data such
654 as those provided by bio-loggers. Similarly, state-space models and behavioural change-point
655 analysis would be enhanced greatly by careful incorporation of data on acceleration or energy
656 expenditure. Indeed, the behavioural states in these models are often "hidden" (as in "hidden
657 Markov model") but the sort of bio-logging data described in this review may be able to shed
658 light on these states more directly. This will be a major change in the field and allow
659 markedly improved and biologically relevant understanding to be obtained; compared to any
660 of the even most sophisticated modelling approaches currently used.
661

662 **4. Future developments for optimising the use of bio-logging**
663 So far, we have reviewed the current technologies and techniques available in the bio-logging
664 toolbox, and how we may optimise their use to answer the big questions in ecology through
665 collaborations within the IBF. Here we highlight potential key future developments, across
666 all nodes of the IBF, which would markedly advance the fields of bio-logging and movement
667 ecology.
668

669 *New sensors: from speed measurement to skin-patches*
670 As speed is a key parameter of movement, there is an urgent need for reliable speed sensors
671 without the disadvantages (such as fouling) or limits of propellers, flexible paddles, and Pitot
672 tubes (cf. Shepard, Wilson, Liebsch, et al., 2008). Speed of movement exposes animals
673 differentially to conditions and equates to (the square root of) power. New sensors need not
674 be limited to external sampling systems either. Animal skin-associated 'patches' are being
675 increasingly used in lab scenarios to look at physiological variables such as stress hormones
676 and other chemicals (Lee, Bakh, Bisker, Brown, & Strano, 2016), something that would find
677 great resonance in wild animal studies. We see huge scope for cross-fostering between these
678 fields, but there are substantial challenges as many of these applications, such as those
679 developed for human studies (Nikita, 2014; Yang, 2014), require powerful readers that

680 operate at close range, and tend to be severely battery limited. Finally, tags need to be able to
681 drop off more routinely and be recovered reliably over large spatial scales, to obtain the large
682 amount of recorded data. This may also save the animal the stress of being recaptured and
683 having to carry the tags for longer than necessary, with all the tag detriment issues that this
684 engenders.

685

686 *Improved ethical and animal welfare methodologies*
687 Although sensor technology is advancing rapidly, the ethics of bio-logging is still a major
688 concern both in terms of fitting the device, which often requires capture, and the effects of
689 carrying a bio-logger for the study subject. Advancing methodology in capture and
690 consideration of stress by the animal is something that ecologists can work on. Be it reducing
691 handling times, protecting a nest from predators or competitors while the animal is unable to,
692 or even advancing remote tagging methods where the animal does not need to be handled. An
693 additional limitation, is that most devices store data on-board, necessitating recapture of
694 animals and the recovery of the units. Improving the ability of these devices to remotely
695 transmit data would improve their applicability and reduce invasiveness, though may require
696 additional weight in terms of electronics and battery. Of greater concern are tags which
697 require surgical implantation, including heartrate and internal temperature loggers. Though,
698 recent advances have led to the development of surgically implanted sensors even measuring
699 neurological activity, which may further our understanding of the mechanisms behind
700 behaviour, but at what cost for the animal?

701

702 A related key limitation to current bio-logging devices is expressed by the 'measurement
703 effects performance' paradigm (Wilson, Grant, & Duffy, 1986) via, for example, increased
704 movement costs for the animal through additional mass loading or the 'drag' of the device
705 (Barron, Brawn, & Weatherhead, 2010; Vandenabeele et al., 2015) producing non-
706 representative data. There are also other important moral and ethical considerations to animal
707 detriment (Cooke et al., 2017; Wilson et al., 2019), such as cumulative effects (as a result of
708 re-tagging) and long-term effects (decreased survival and/or lifetime reproductive success,
709 which may not be easily evident from short term changes in movement and activity patterns).
710 Thus the current 'rule of thumb' based on 3-5% body weight (for aerial and terrestrial
711 animals respectively) is naïve (Bodey et al., 2018), and will need to be improved using more
712 comprehensive information on tag effects based on physical principles (e.g. via
713 computational fluid dynamics to account for drag; Kay et al., 2019), considering also the

714   often neglected effects of tag attachment itself (Vandenabeele et al., 2014). In the meantime,

715   certainly researchers will have to better exploit the ongoing miniaturisation to reduce the

716   relative mass of the devices attached to animals (Portugal & White, 2018). Equally important,

717   researchers should consider if a new tagging study is necessary, or if the question can be

718   answered using existing published data or through data sharing, which will require the

719   development of markedly improved data standards for bio-logging data (see previous section;

720   Figure 3).

721

722   *Lifetime tracking, real-time processing and remote data transmission*

723   As bio-logging technology continues to advance, the ability to study an individual or

724   population throughout their entire life from conception to death becomes a more realistic

725   possibility. Such large-scale tagging has major ethical implications, as not only a small subset

726   is affected but an entire group, community or population. Especially for similar large-scale

727   questions, researchers would benefit from enhanced bandwidth for transmitting data (*cf.*

728   O'Donoghue & Rutz, 2016), an element that is already being trialled within the ICARUS

729   system (Wikelski et al., 2007). In tandem with this comes smart on-board data-processing

730   (e.g. Cox et al., 2018) which has the potential to markedly increase the temporal and

731   taxonomic range of data which can be collected. The combination therein of real-time

732   processing and transmission of data will not only enable scientists to dynamically adapt

733   experiments, but has applications in conservation and management.

734

735   *Improving the theoretical and mathematical foundations of movement ecology*

736   Perhaps the most exciting aspect of bio-logging is that the data-rich approach driven by

737   animals will not only help us to understand why animals do what they do, pinpointing drivers

738   that range from internal state responses to pan-ocean basin atmospheric conditions, but

739   thanks to an improved mechanistic understanding, we might actually be able to predict

740   animal responses to future conditions. To do so will require a large improvement in the

741   theoretical and mathematical foundations of movement ecology, to include the rich set of

742   high-frequency multivariate data, which greatly expand the fundamentally limited and coarse

743   data that could be collected using location-only technology such as GPS. In particular, there

744   is a clear synergy between local (small-scale) information provided by sensors and large-

745   scale information provided by, for example, remote sensing data. How to link and predict

746   processes occurring across different scales is a central question in ecology (Levin, 1992) yet

747   difficult to address, with the key issues being to identify the correct mesoscopic scale

748   connecting microscopic processes to macroscopic patterns. This is the case even for 'simple'

749   physical systems constituted of identical particles, whereas biological systems are instead

750   fundamentally characterised by additional intra- and inter-specific heterogeneity. Movement

751   ecologists therefore have to deal with processes which span multiple scales of spatio-

752   temporal and biological complexity (Torney, Hopcraft, Morrison, Couzin, & Levin, 2018).

753   Hence, demanding yet exciting challenges lie ahead for integrating novel bio-logging data

754   with ecological questions. We may now have access to vastly improved information for wild

755   animal biologists to predict processes.

756

757   *Improved multi-disciplinary collaborations*

758   Collaboration is key to the framework's success as a tool for optimisation of bio-logging

759   studies. At the same time, ecologists can feed new developments back to other disciplines,

760   e.g. as inspiration for new theorems (Cohen, 2004; Sturmfels, 2005), or for biologically

761   inspired engineering (Bionics), such as new models of navigation inspired by ants (Esterley,

762   McCreery, & Nagpal, 2017) or improved collective decision making in robot swarms (Ebert,

763   Gauci, & Nagpal, 2018). Indeed, actions to bring together multi-disciplinary groups of

764   experts are gathering momentum in movement ecology; these include the EU COST actions

765   from MOVE to develop improved methods for knowledge discovery from moving objects

766   and big data (www.cost.eu/COST_Actions/ict/IC0903) with similar initiatives in the

767   European Network for Radar Surveillance of Animal Movement (http://www.enram.eu/), the

768   Special Interest Group in Movement Ecology of the British Ecological Society

769   (www.britishecologicalsociety.org/membership-community/special-interest-

770   groups/movement-ecology/) and the International Bio-Logging Society (www.bio-

771   logging.net/).

772

773

774   **Conclusion**

775   We have i) reviewed how to optimise the use of bio-logging techniques for ecologists to be

776   able to take full advantage of the paradigm-changing opportunities of bio-logging sensors for

777   ecological research and ii) synthesised this into an Integrated Bio-logging Framework (IBF)

778   for movement ecology research. We highlighted the many new and often unexplored

779   opportunities to address biological questions using the most appropriate sensors and sensor-

780   combinations, especially using multi-sensor approaches, a new frontier in bio-logging

781   research. Given the technological complexities and rapid pace of advancement of the field,

782　however, establishing multi-disciplinary collaborations will be paramount for ecologists –

783　and at the same time, the latter can thereby more efficiently guide future technological and

784　methodological advancements to address biological questions. Closely linked to the issue of

785　matching ecological questions with sensors, is devising a good experimental design up front.

786　This involves multiple closely connected challenges, from tag design and sampling regime, to

787　the important related ethical and animal welfare considerations, and the challenges of data

788　sharing. Linking new bio-logging data types to the most adequate analytical techniques

789　presents many new and often unsolved issues in particular, and will require multi-disciplinary

790　collaborations to tackle the 'big data' problem, and improve the theoretical and mathematical

791　foundations of movement ecology. The tasks ahead are challenging, but a clear potential

792　exists for a vastly improved mechanistic understanding of animal movements and their role in

793　ecological processes, from which we can build unprecedented and realistic predictive models.

794

795

811

812　**Author contributions**

813　The manuscript was conceived by LB in discussion with all authors at BES Move 2018. All

814　authors wrote the manuscript, led by HJW and LAT, aided by RPW, CR and LB. The authors

815　declare no conflicts of interest.
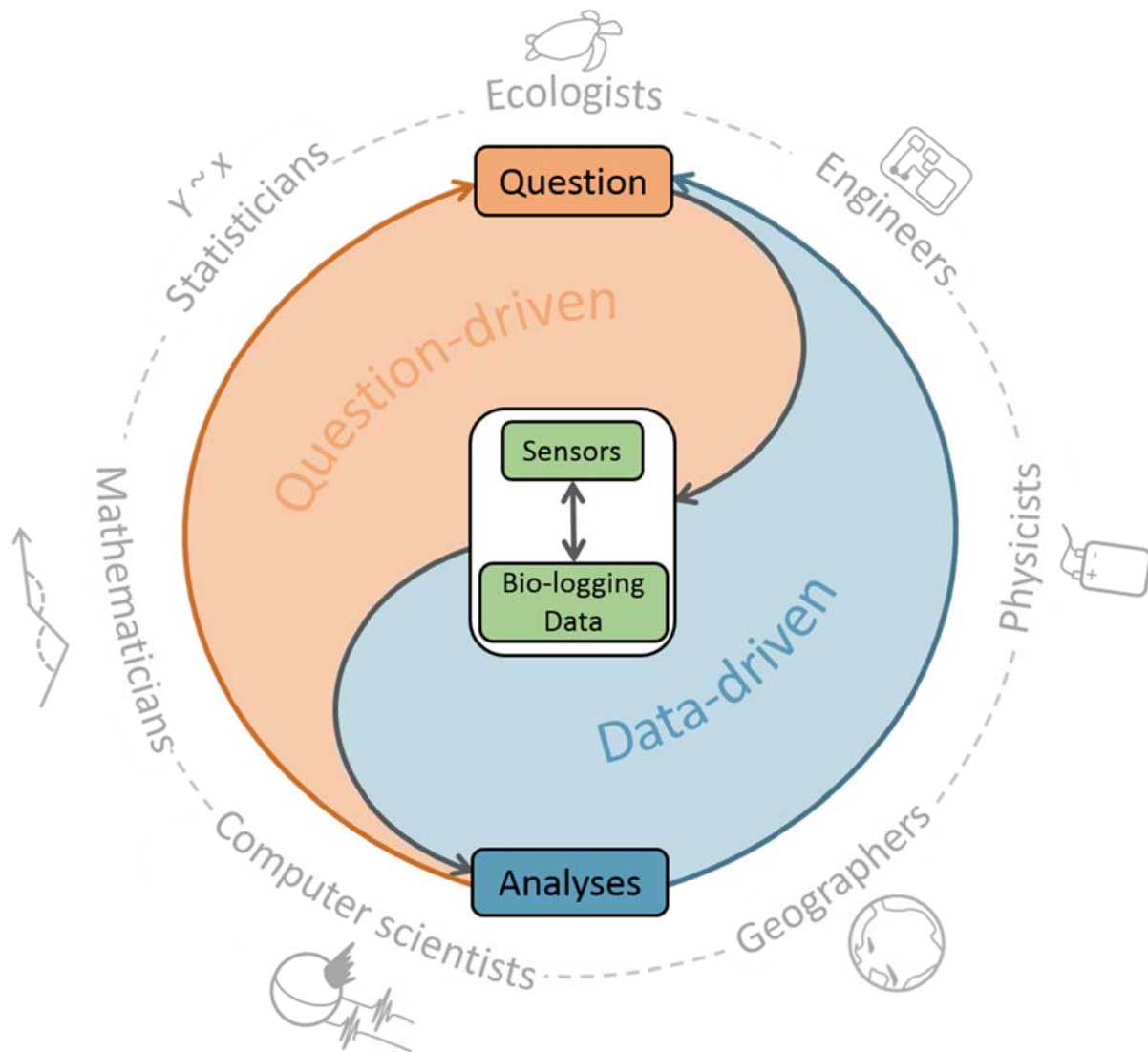
816

817 **Tables and Figures**

818

819 Table 1: Summary table of the current bio-logging sensors available, beyond classic location

820 sensors. The detailed application and description of sensors is provided in SI Table 1.

821

Sensor type	Examples	Description	Relevant questions	Optimisation
Location	Animal-borne radar, pressure, passive acoustic telemetry, proximity sensors	Location based on receiver location	Space use; interactions	Use in combination with the behavioural sensors below; Create visualisations to facilitate interpretation of 3D space use and interactions
Intrinsic	Accelerometer, magnetometer, gyroscope, (gyrometer)	Patterns in body posture, dynamic movement, body rotation and orientation.	Behavioural identification; internal state; 3D movement reconstruction (dead-reckoning); energy expenditure; biomechanics; feeding activity; space use	Use in combination with other intrinsic sensors to build up detail of behaviour and/or 3D path reconstruction; Increased sensitivity to detect micro-movements or stress-related activity; high resolution (temporal and spatial) environmental data may improve accuracy of path reconstruction (e.g. in relation to environmental flow, wind or current data)
	Heart rate loggers, stomach temperature loggers, neurological sensors, flexible speed paddle, pitot tube, speed paddles	Measures of activity.		
	Microphone, hall sensors,	Specific behaviour e.g. limb movement and vocalisations		
Environment	Temperature	Ambient	Space use; energy expenditure; external factors; interactions	In situ remote sensing; arrays to localise animals; visualisations to provide context and understanding of interactions
	Microphone, proximity sensors, video loggers	Record external environment e.g. soundscape		

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826　Figure 1: ***The Integrated Bio-logging Framework (IBF) for optimal use of bio-logging in***
827　***movement ecology.*** *Researchers may take a question-driven approach, beginning with a*
828　*hypothesis, then selecting the appropriate sensor and analysis techniques. Alternatively, a*
829　*data-driven approach can be taken, by allowing existing data to inform further hypotheses*
830　*and data collection. The framework operates via collaboration between disciplines in a*
831　*system of feedback loops, though these collaborative links are not exclusive to any particular*
832　*node.*

833
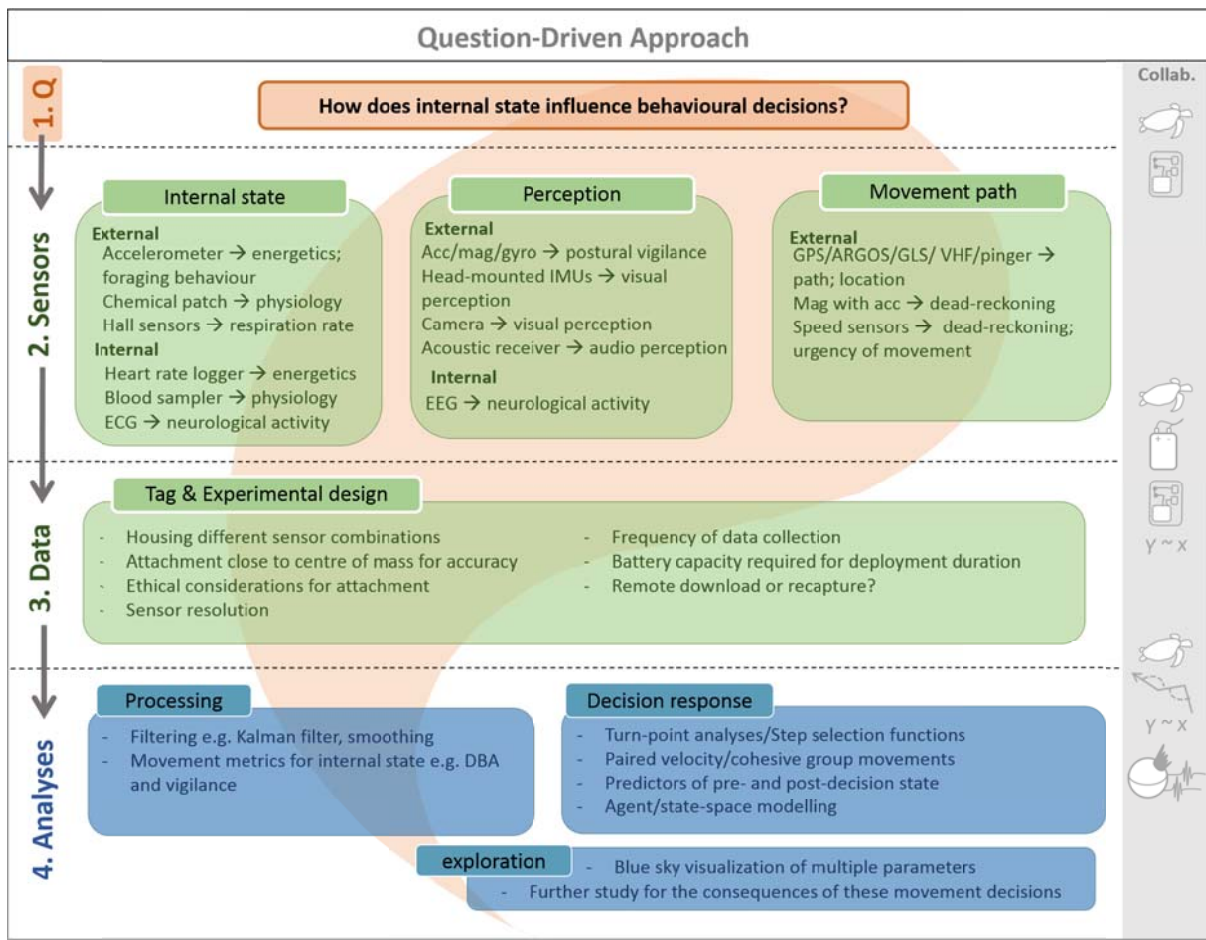
834
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836 Figure 2: *A question-driven approach to the IBF for optimal study design using bio-*
837 *logging. In this example, ecologists begin with their question of focus (top of Figure 1), in*
838 *this case an investigation into the effect of internal state on movement decisions, and select*
839 *the appropriate external and internal sensors for data collection. Here, sensors should be*
840 *sensitive to different aspects of an animal's movement that relate to their internal state,*
841 *perceived information and the movement that may result from a particular decision. Selection*
842 *of the sensors requires strong collaboration between ecologists and engineers (right-hand*
843 *symbols). Simultaneously (bottom of Figure 1), ecologists should work with those analysing*
844 *the data (e.g. physicists, mathematicians, statisticians, computer scientists) in the process of*
845 *designing the data collection, to ensure the correct data are gathered that can answer the*
846 *question using the analytic tools available.*
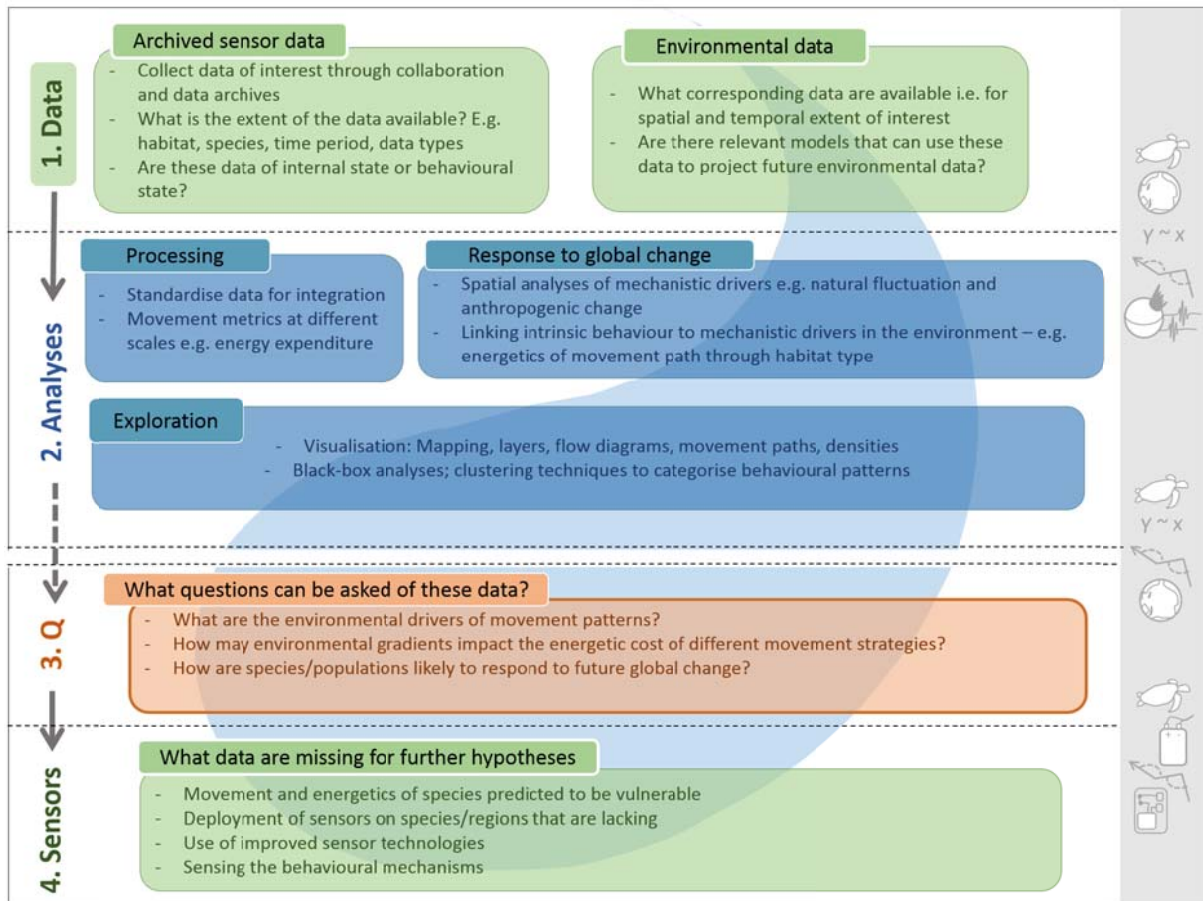
Figure 3: ***A data-driven approach to the IBF for optimal study design using archived bio-logging data.*** *In this example, ecologists begin by selecting appropriate data types for the study of movement patterns in relation to environmental measures at local and global scales. Understanding and predicting how animals respond to global change, including climate and land-use change, requires multiple data collected over a range of temporal and spatial scales. In this case, ecologists start at the central nodes of the IBF (Figure 1) to collate archived data and collaborate with mathematicians, statisticians and geographers (right-hand symbols) to implement the appropriate processing and analytical techniques to interrogate the data and identify patterns by which several questions may be approached. Following this, ecologists may work with other disciplines to deploy additional bio-logging sensors to collect data that complement the shared data.*
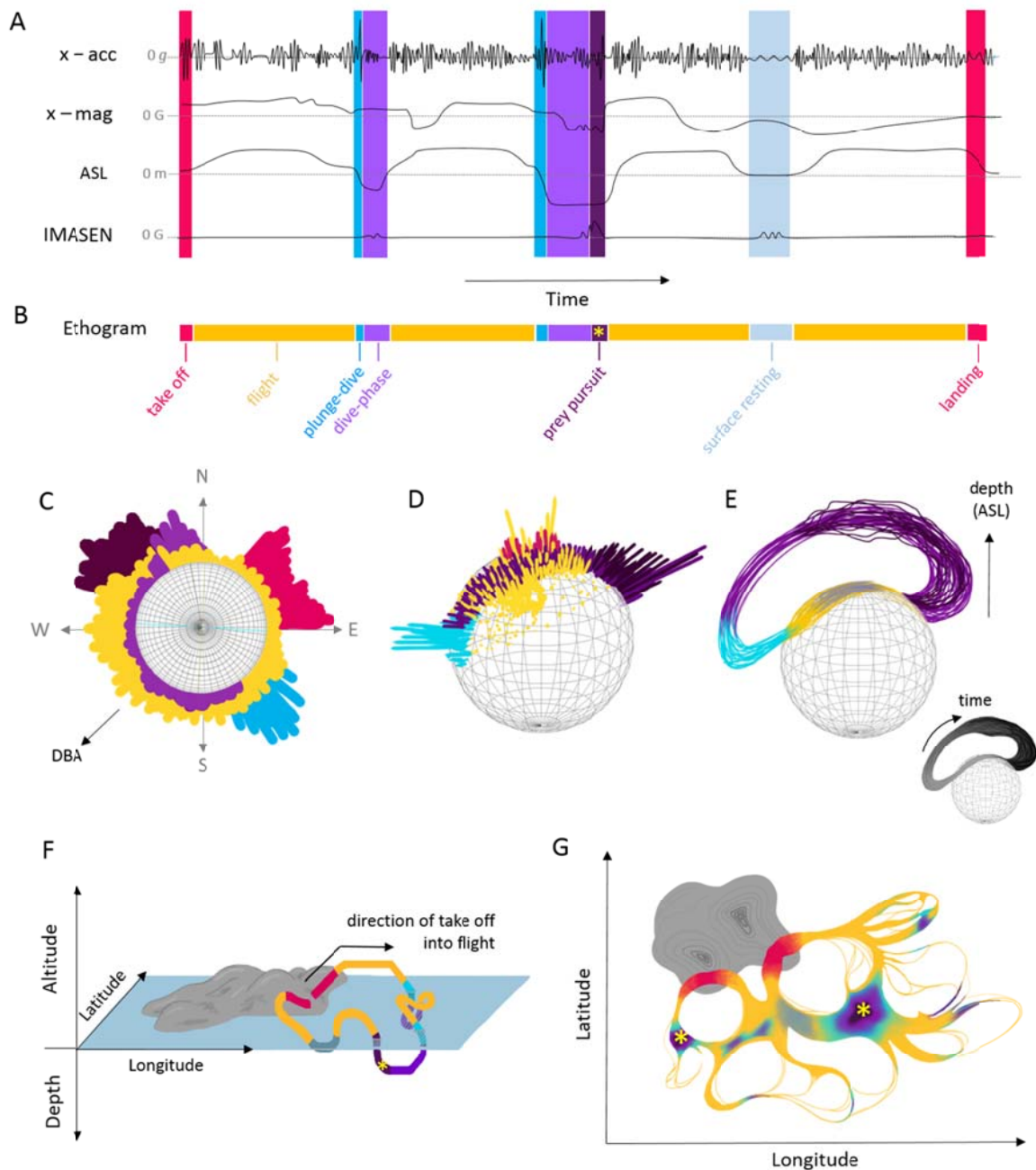
861   Figure 4: ***Visualisation of sensor and location data.*** *A number of schematic plots of varying*

862   *axes and information types to visualise data of a seabird in flight that plunge-dives in pursuit*

863   *of prey. A) Logged sensor outputs (acceleration (g), magnetometry (µT), altitude above sea*

864   *level (m) derived from pressure data (kPa) and the inter-mandibular angle sensor IMASEN*

865   *output (µT)) in a time series plot. Peaks in dynamic acceleration are associated with wing*

866   *beats during take-off (red) and in flight (yellow), as well on impact with the sea surface in*

867   *plunge-dives (aqua blue). During the dive, as indicated by the negative altitude above sea*

868   *level (ASL; purple) the bird may pursue prey (dark purple), as indicated by increased*

869   *variation in acceleration and heading, from the magnetometer output. A successful prey*

870 *capture attempt is evident in the peaks in the IMASEN signal output, as the bird opens its bill*

871 *to capture the prey (yellow asterisk). B) The behaviours are classified and presented in an*

872 *ethogram to show temporal variation in behaviour (this serves as a key for the schematic).*

873 *Further to these time series plots, different sensor outputs can be combined, along with*

874 *derived metrics, in various multi-axes visualisations to reveal patterns in behaviour. We*

875 *present three examples (C-E) for data visualisation in multi-dimensional space and two for*

876 *geographic space (F-G): C) a circular plot of heading on an m-sphere (magnetometry;*

877 *Williams et al., 2017), where height of the bar is the magnitude of the extent of movement*

878 *(DBA), the most active behaviours for this bird are foraging and diving, which occur at*

879 *opposite headings; D) a g-sphere (static acceleration data) or Dubai plot, where a frequency*

880 *histogram of static acceleration is resolved in tri-axial space (Wilson et al., 2016) and peaks*

881 *show the most common postures for each behaviour; E) a g-sphere where distance from the*

882 *surface of the sphere is relative to the depth below sea level, where colour indicates different*

883 *behaviours in the dive, so that through the dive there is a shift in posture, and a greater*

884 *variation in posture and depth during the prey pursuit (coloured by time in greyscale, bottom*

885 *right); F) 3D movement path during for the foraging trip; G) 2D flow visualisation of*

886 *foraging path, where thicker paths are more commonly used for the different behaviours*

887 *(Verbeek, Buchin, & Speckmann, 2011).*

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