

## 1 **Optimising the use of bio-loggers for movement ecology research**

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36

37 **Abstract**

- 38 1. The paradigm-changing opportunities of bio-logging sensors for ecological research,  
39 especially movement ecology, are increasingly highlighted, but the crucial questions of  
40 how best to match the most appropriate sensors and sensor combinations to specific  
41 biological questions, and how to analyse complex bio-logging data, are mostly ignored.  
42 2. Here, we fill this gap by reviewing how to optimise the use of bio-logging techniques  
43 to answer questions in movement ecology and synthesise this into an Integrated Bio-  
44 logging Framework (IBF).  
45 3. We highlight that multi-sensor approaches are a new frontier in bio-logging, whilst  
46 identifying current limitations and avenues for future development in sensor  
47 technology.  
48 4. We highlight the importance of efficient data exploration, and more advanced multi-  
49 dimensional visualisation methods, combined with appropriate archiving and sharing  
50 approaches, to tackle the big data issues presented by bio-logging. We also discuss the  
51 challenges and opportunities in matching the peculiarities of specific sensor data to the  
52 statistical models used, highlighting at the same time the large advances which will be  
53 required in the latter to properly analyse bio-logging data.  
54 5. Taking advantage of the bio-logging revolution will require a large improvement in the  
55 theoretical and mathematical foundations of movement ecology, to include the rich set  
56 of high-frequency multivariate data, which greatly expand the fundamentally limited  
57 and coarse data that could be collected using location-only technology such as GPS.  
58 Equally important will be the establishment of multi-disciplinary collaborations to  
59 catalyse the opportunities offered by current and future bio-logging technology. If this  
60 is achieved, clear potential exists for developing a vastly improved mechanistic  
61 understanding of animal movements and their roles in ecological processes, and for  
62 building realistic predictive models.

63

64 **Key words:** Bio-logging, multi-disciplinary collaboration, movement ecology, multi-sensor  
65 approach, big data, data visualisation, Integrated Bio-logging Framework, accelerometer, GPS.

66

67 **Introduction**

68

69 Movement is a fundamental aspect of life, intrinsically linked to almost every ecological and  
70 evolutionary process, from the acquisition of food, through reproduction and survival, to  
71 species distributions and community structure. Decades of technological developments have  
72 created vast possibilities in terms of data collection to study the movement of organisms, from  
73 VHF (Kenward, 2001), ARGOS and GPS technology (Kays, Crofoot, Jetz, & Wikelski, 2015;  
74 Tomkiewicz, Fuller, Kie, & Bates, 2010; Weimerskirch, 2009), to reverse GPS technology  
75 (Weiser et al., 2016) and dedicated satellite systems for tracking animals around the globe  
76 (ICARUS, see Wikelski et al., 2007), to sensor and acoustic receiver networks for animal  
77 tracking (Duda et al., 2018; Hoenner et al., 2018). In tandem, ecologists have driven a  
78 revolution in bio-logging sensor technology, motivated by the need to gather behavioural and  
79 ecological data that cannot be obtained through direct observation. This revolution has resulted  
80 in the development and use of a variety of sensors to observe the unobservable, including *inter*  
81 *alia*: accelerometers, magnetic field sensors, gyrometers, temperature and salinity sensors,  
82 further complemented by video cameras and proximity-loggers (Rutz & Hays, 2009) - see SI  
83 Table 1. The combined use of multiple sensors can provide indices of internal ‘state’ and  
84 behaviour, reveal intraspecific interactions, reconstruct fine-scale movements and even  
85 measure local environmental conditions (Rutz & Hays, 2009; Wilson et al., 2014). However,  
86 with increasing sensor possibilities comes a new challenge: pinpointing the appropriate  
87 information to collect, and finding efficient ways to do so.

88

89 It is hardly surprising, therefore, that there is an increasing number of high-profile reviews that  
90 showcase the paradigm-changing opportunities offered by animal-attached technology for  
91 ecological research (Hussey et al., 2015; Kays et al., 2015; Wilmers et al., 2015). Within these  
92 reviews, however, there exists scant treatment of how best to match the most appropriate  
93 sensors and sensor combinations to specific biological questions. As a result, ecologists have  
94 tended to use statistical methods *post hoc* to overcome the limitations of specific sensor data,  
95 including smoothing methods such as Kalman filtering and state-space models or machine-  
96 learning approaches applied to positional and accelerometer data. Similarly, although new  
97 analytical methods show great promise, such as the use of machine-learning to identify  
98 behaviours from tri-axial acceleration data (Nathan et al., 2012) or Hidden Markov Models  
99 (HMMs) to infer hidden behavioural states (Leos-Barajas et al., 2017), no clear guide exists to  
100 promote best practices. Such a guide would allow ecologists and statisticians to strike a balance

101 between overly simplistic and complex models to deal with the vagaries of specific sensor data,  
102 for example the limitations of accelerometer data (see also Patterson et al., 2017). We aim to  
103 fill this gap by considering how to optimise the use of bio-logging techniques to answer key  
104 questions in movement ecology. In doing so, we identify four critical areas – questions, sensors,  
105 data, and analysis – and related opportunities for multi-disciplinary collaborations, and  
106 synthesize these into an Integrated Bio-logging Framework (IBF) to aid the decision-making  
107 process for ecologists. We then review the technologies and methodologies available to  
108 ecologists to make the links between nodes of the framework. We first consider how best to  
109 address biological questions using the most appropriate sensors while identifying current  
110 technological limitations. Second, we review the challenges and opportunities of linking new  
111 data types obtained from bio-logging sensors to the most adequate analytical techniques. We  
112 discuss issues relating to dealing with large, complex datasets, the fundamental properties of  
113 the new data types that can be collected, and the challenges of archiving and sharing bio-  
114 logging data. Finally, we discuss the value of multi-disciplinary collaborative links to optimise  
115 the opportunities offered by current and future bio-logging technology.

116

### 117 **The Integrated Bio-logging Framework**

118 Four areas are critical for optimal bio-logging study design: questions, sensors, data, and  
119 analysis. We connect these via three-nodes in a cycle of feedback loops, linked by multi-  
120 disciplinary collaboration (Figure 1). Ecologists can work their way through the IBF to develop  
121 their study design – typically, this will start with the biological question, but the pathways will  
122 differ if, for example, using a question/hypothesis driven (blue) or data-driven (orange)  
123 approach. Figures 2 and 3 provide two such pathway examples.

124

125 Furthermore, bio-logging has become so multifaceted and complex that no-one can be a  
126 ‘master of all trades’, hence, establishing multi-disciplinary collaborations is key (as for other  
127 disciplines, Peters et al., 2018), and this idea is at the basis of the IBF. For example, at the study  
128 inception phase, dependent on the biological problem addressed, physicists and engineers can  
129 advise on sensor types, their limitations and power requirements, while mathematical  
130 ecologists and statisticians can aid in framing the study design and modelling requirements for  
131 specific questions (see Figure 2). Development of bio-logging tags is the result of  
132 collaborations between engineers, physicists and biologists, while visualisation and analytical  
133 methods for dealing with data are aided by interactions with computer scientists, geographers,  
134 statisticians and mathematicians (see Figure 3). On the other hand, ecologists can guide

135 researchers from the other disciplines towards the key methodological hurdles and  
136 technological limitations which are hindering progress and need to be addressed.

137

138 We now review the literature regarding questions, sensors, data and analyses, and exemplify  
139 the links between the nodes of the IBF. We conclude by highlighting areas for future  
140 development.

141

## 142 **1. From questions to sensors**

143 Researchers can choose between an ever-increasing number of different bio-logging sensors  
144 (Table 1, SI Table 1). Following the adage that experimental design should be guided by the  
145 questions asked (e.g. Fieberg & Börger, 2012; Hebblewhite & Haydon, 2010), sensor choice  
146 is clearly critical. Here, we consider sensor selection within the general scheme of key  
147 movement ecology questions posed by Nathan et al. (2008) and provide an example for the use  
148 of the IBF in a question-driven approach to study design.

149

### 150 *1.1 Why is the animal moving?*

151 Animals make behavioural decisions based on their internal ‘state’ (physiological and  
152 psychological condition), and external biotic and abiotic factors (Nathan et al., 2008).  
153 Identifying and quantifying how internal state may drive behaviour is non-trivial, and can often  
154 only be indirectly inferred (Getz & Saltz, 2008). Some aspects of animals’ internal state have  
155 been investigated using accelerometers which are sensitive to micro-movements and postures  
156 indicative of chemical, disease, and affective states (Downey et al., 2017; Wilson et al., 2014),  
157 including vigilance behaviour, a stress-related response (Kröschel, Reineking, Werwie, Wildi,  
158 & Storch, 2017). Alongside accelerometers, other key sensors that can provide insights into  
159 internal state include heart rate, internal temperature, and neurological sensors (Rattenborg et  
160 al., 2016). For example, heart rate loggers to investigate the interplay between ecological  
161 pressures and energetic strategies were used by Bishop et al. (2015) in bar-headed geese (*Anser*  
162 *indicus*) and O’Mara et al. (2017) in fruit-eating bats (*Uroderma bilobatum*). As another  
163 example, Ditmer et al. (2018) used heart rate loggers to investigate how American black bears  
164 (*Ursus americanus*) perceive the risks of crossing roads. Research on humans has demonstrated  
165 that bio-loggers can measure a suite of physiological variables relating to internal state (Nikita,  
166 2014; Yang, 2014) and the development of similar systems for wild animals is increasing;  
167 examples include animal-borne blood sample collection devices for stress hormones in seals

168 (Takei et al., 2016), other hormonal sensors (Landry et al., 2014), and internal chemical  
169 detection nanosensors for freely moving animals (Lee et al., 2018) .

170

171 The greatest insight into state-driven movement is likely to be gained from multi-sensor  
172 approaches (e.g. Wilson, Littman, Halpin, & Read, 2017), especially combining both  
173 physiological and/or neurological sensors with position-determining systems (Figure 2). For  
174 example, Vyssotski et al. (2006) simultaneously measured pigeon (*Columba livia*) movement  
175 and electrical brain activity using a miniaturised GPS combined with an  
176 electroencephalography logger, while Dunn et al. (2016) obtained a brain-wide mapping of  
177 neural activity of zebrafish (*Danio rerio*) during movement. The use of neurological sensors to  
178 monitor brain activity in freely moving animals is a relatively new advancement (e.g.  
179 Rattenborg et al., 2016; Skocek et al., 2018). Such multi-sensor developments are helping to  
180 meet the challenge of linking internal state, as a proximate cause of movement, to ultimate  
181 evolutionary causes (Nathan et al., 2008). However, there are important ethical considerations  
182 to be raised, especially for surgically implanted sensors (e.g. see the example of frigatebirds  
183 below, Rattenborg et al., 2016).

184

185 Alongside the internal state, what is happening in the environment is the other prime driver of  
186 animal movement. Global environmental data can be recorded through satellite remote sensing,  
187 and bio-loggers now routinely collect local environmental data both biotic and abiotic (Table  
188 1; SI Table 1), thus a major aspiration is to link such data to movement. Though whilst  
189 ecologists can access an increasing amount of remote-sensed environmental data, linking them  
190 to location data is usually difficult, as environmental data are obtained at different, generally  
191 coarser, spatiotemporal scales than movement data (Dodge et al., 2013). Remelgado et al.  
192 (2019) recently developed a new pixel-based approach, combined with data mining and  
193 visualization, to help ecologists efficiently deal with differences in the spatial, temporal and  
194 thematic resolutions between environmental data from remote sensing and GPS location data;  
195 yet the problem persists with high frequency bio-logging data.

196

197 Depending on the question asked, it may be necessary to use modelling to derive high-accuracy  
198 dynamic maps of environmental conditions (e.g. vertical wind; see Scacco, Flack, Duriez,  
199 Wikelski, & Safi, 2019), or to use drones or LiDAR, to build ultra-high resolution, 2- and 3-  
200 dimensional maps of the study area (e.g. to investigate movement costs due to elevation or to  
201 quantify vegetation quality for optimal foraging questions). Importantly, bio-loggers allow the

202 collection of high-frequency environmental data at the local scale experienced by the animals,  
203 such as temperature, light intensity, and wind or current velocity (Block, 2005; Dodge et al.,  
204 2013; Piersma & Lindström, 2004). This may be complemented by implanted sensors such as  
205 core body temperature sensors (e.g. when studying heat stress questions), combined with  
206 sophisticated use of meteorological data to estimate the so-called wet bulb globe temperature  
207 index (WBGT), a key measure of heat stress (Dimiceli, Piltz, & Amburn, 2011).

208

209 In terms of the biotic environment', an animal's movement decisions are likely to be influenced  
210 by interactions with conspecifics and heterospecifics and again, there are certain combinations  
211 of sensors that can record and help identify these interactions. There are two main approaches  
212 to remotely record the social contact between free-ranging animals: indirect and direct  
213 encounter mapping (see Bettaney, James, St Clair, & Rutz, 2015; Krause et al., 2013). Indirect  
214 encounter mapping can be achieved either with high-resolution tracking of subjects, or with  
215 the use of tags that transmit to, or that are detected by, fixed receiver stations at specific  
216 locations (e.g., coded VHF radio-tags or PIT/RFID tags). In both cases, the co-occurrence of  
217 animals is inferred at the data analysis stage. Direct encounter mapping, on the other hand,  
218 requires the use of proximity loggers (transceiver tags that both transmit and receive radio  
219 signals between animals) or camera tags (Hooker, Barychka, Jessopp, & Staniland, 2015), to  
220 create reciprocal records of social encounters (Bettaney et al., 2015; Krause et al., 2013).  
221 Proximity-loggers can be used for addressing a variety of biological questions, and have the  
222 advantage over cameras (e.g. Takahashi et al., 2004) that they survey in all directions (even  
223 though precise directional and distance information is often not collected), but their key  
224 strength lies in charting social associations of a large number of subjects of known identity, to  
225 reconstruct group, community, or even population-level social networks. Proximity sensors  
226 can also be used to record interspecific encounters, for example between predators and their  
227 prey, between different disease hosts, or in mixed groups of foraging or migrating animals.  
228 Some systems are set up as wireless sensor networks where animal-mounted sensors not only  
229 communicate with other sensors, but also with (a large number of) stationary receiver (base)  
230 stations (Rutz et al., 2012). This enables near real-time data transmission, which is key to  
231 evaluating system performance and to planning and monitoring experimental manipulations  
232 (St Clair et al., 2015).

233

234 A particular type of interspecific interaction occurs when animals interact with human  
235 activities, which can strongly affect animal movements (e.g. Tucker et al., 2018). An

236 interesting development is animal-borne radar detectors, which detect signals from emitting  
237 radars in the surroundings and can be used in combination with a tracking device to log the  
238 occurrence of structures along an animal's movement path (Table 1; SI Table 1). This has  
239 facilitated the study of seabird-fishing vessel interactions, quantifying attraction, attendance  
240 and foraging behaviour (Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018).

241

### 242 *1.2 Where is the animal going?*

243 ARGOS, GPS and related satellite and global navigation systems, as well as acoustic tracking  
244 arrays and geolocators, have revolutionised information on animal locations and movements  
245 (Kays et al., 2015). Bio-logging sensors, particularly in combination with such locational  
246 tracking-devices, can further help detect where animals move. For example, Hedenstrom et al.  
247 (2016) combined geocator and accelerometer tags to record flight behaviour of migrating  
248 swifts, and Shipley, Kapoor, Dreelin, & Winkler (2018) used micro barometric pressure  
249 (altitude) sensors (<0.5 g) to uncover the aerial movements of migrating birds. A key limitation  
250 of telemetry devices is that transmission technology can fail, such as when canopy cover  
251 impedes GPS satellite fixes (Rempel, Rodgers, & Abraham, 1995). However, with the  
252 combined use of tri-axial orientation, posture/activity and elevation/depth recording sensors it  
253 is possible to reconstruct animal movements in 2D and 3D using a dead-reckoning procedure,  
254 irrespective of transmission conditions (Bidder et al., 2015; Bramanti & Dall'Antonia, 1988).  
255 This uses the speed (including speed-dependent dynamic body acceleration (DBA) for  
256 terrestrial animals; Bidder, Qasem, & Wilson, 2012), combined with animal heading (from  
257 magnetometer data) and change in altitude/depth (pressure data) to calculate the successive  
258 movement vectors (oriented steps) from a known starting position. The process gives  
259 extraordinarily finely resolved relative movement (it can, for example, determine how many  
260 times a dog has walked around a lamppost) but it can accumulate errors over time, especially  
261 in fluid media with current flow. Therefore, data used in dead-reckoning need correcting with  
262 frequent ground-truthing, such as by a GPS unit (Bidder et al., 2015). GPS-enabled dead-  
263 reckoning is an incredibly powerful combination of sensor systems which may become  
264 paradigm-shifting within animal movement studies. With this, researchers will have access to  
265 multiple scales of movement and seamless animal movement descriptors and will be able to  
266 identify true turn-points (Potts et al., 2018; see Figure 2 and analyses below). In turn, the  
267 improved track trajectory should allow us to connect behaviour to landscape ecology and  
268 population dynamics with increased confidence (Morales et al., 2010).

269



270 *1.3 How is the animal moving?*

271 At the smallest scale (locomotion), animals move according to their anatomy and the  
272 biomechanics that this engenders, with obvious differences between animals operating in fluid  
273 media (air or water) or on the ground (Biewener & Patek, 2018). In essence, locomotion is  
274 manifested by particular patterns of movement by the various body parts (most notably limbs)  
275 so that motion-sensitive transducers can provide critical information with respect to the pattern  
276 and intensity of movements and thereby derive critical whole-animal movement parameters  
277 such as speed and direction. The primary sensors used for this include accelerometers,  
278 magnetometers and gyrometers (often collectively grouped within inertial measurement units  
279 [IMUs]; e.g. Noda, Kawabata, Arai, Mitamura, & Watanabe, 2014), Accelerometers and  
280 magnetometers can be used to infer the 3D posture and orientation (i.e. azimuth, elevation  
281 angle and bank angles; see SI Table 1 for a glossary of terms) during locomotion, whereas  
282 gyrometers provide direct measures of yaw, pitch and roll (see Benhamou, 2018 for the  
283 mathematical relationships between these parameters). In addition, various iterations of speed-  
284 detecting systems, such as anteriorly mounted propellers (Ropert-Coudert et al., 2000;  
285 Watanabe et al., 2008), flexible paddles (Shepard, Wilson, Liebsch, et al., 2008), and Pitot  
286 tubes are also used (Taylor, Reynolds, & Thomas, 2016). Importantly, the speed at which an  
287 animal is moving provides information on the urgency with which the movement is being  
288 undertaken. When moving animals deviate from minimum cost of transport (cf. Schmidt-  
289 Nielsen, 1972), it indicates time-based selection pressures that incite animals to move non-  
290 optimally in energetic terms; the reasons for which may be critical for lifetime fitness and only  
291 become apparent *post hoc* (e.g. Shepard, Wilson, Quintana, Laich, & Forman, 2009). Sensors  
292 allow to quantify the energetics of animal locomotion for such issues, as well as record  
293 information for understanding the costs and benefits of behaviours. Several sensors provide  
294 proxies for oxygen consumption ( $VO_2$ ), including heart rate loggers (Green, 2011) and tri-axial  
295 accelerometers through the computation of dynamic body acceleration (DBA; reviewed in  
296 Wilson et al., accepted). Indeed, the continued refinement of these proxies of power use, one  
297 of the most fundamental currencies in the animal kingdom, will be pivotal in providing critical,  
298 missing information within previously established movement frameworks such as optimal  
299 foraging (McNamara & Houston, 1986; Pyke, 1984).

300

301 Sensors that detect body movements may also provide key information relating to  
302 biomechanical questions, such as how stroke frequency relates to stroke amplitude. For  
303 example, magnets used with Hall sensors (sensors detecting magnet-transducer paired

304 magnetic field properties; Hall, 1879 - see S1 Table 1) can quantify the amplitude, angular  
305 velocity and frequency of limb movements of marine mammals (Wilson & Liebsch, 2003),  
306 providing insights into energy-saving mechanisms (Nassar, Jackson, & Carrier, 2001). Animal-  
307 borne video or audio may provide similar information, for example, being able to relate flipper  
308 beat frequencies in green turtles (*Chelonia mydas*; Hays, Marshall, & Seminoff, 2007) and  
309 emperor penguins (*Aptenodytes forsteri*; van Dam, Ponganis, Ponganis, Levenson, & Marshall,  
310 2002), to dive strategies. Hall sensors can also measure respiration rates and extent of  
311 inhalation, heart rates, and even patterns of defaecation, providing information on the optimal  
312 breathing strategies and rates of digestion (Wilson et al., 2003, 2004), cases where mounted-  
313 accelerometers would be limited due to movement being mainly translocational. In addition,  
314 these behaviours can also be detected from on-board videos. Yet few studies use these  
315 techniques, perhaps because researchers find the magnetic field intensity drop off with distance  
316 intractable and because, at the time the studies were published, it was not possible to study  
317 angular changes between magnet and sensor, if distances were held constant. Inertial  
318 measurement units (IMUs) have changed this, so we think that the future of miniature IMUs  
319 holds promise for researchers to document minute changes in body movement and for  
320 quantifying motion capacity from limb movements.

321

#### 322 *1.4 What is the animal doing?*

323 Allocating behaviours to space is key to understanding animal niche requirements and the link  
324 between behaviour and fitness consequences. Since the work by Yoda et al. (1999) using  
325 accelerometers to determine animal behaviour, there is a rich and varied literature that  
326 documents increasingly successful methodologies for determining animal behaviour from  
327 various sensor data, especially accelerometers (Nathan et al., 2012; Shepard, Wilson, Quintana,  
328 et al., 2008) and magnetometers (Williams et al., 2017). Thus, it is now possible to extract a  
329 remarkable amount of information regarding behaviour beyond that of limb and body part  
330 movement as detected from tri-axial sensors as described above.

331

332 In particular, quantifying the type and amount of food ingested by animals is essential to  
333 answering some of the “big questions” in movement ecology such as how animals manage  
334 their energy budgets in the wild (cf. Krebs & Davies, 1978). For example, combining GPS and  
335 DBA measures derived from tri-axial accelerometers, allows us to better understand the  
336 energetics underlying prey capture behaviour of large terrestrial predators (Wilmers, Isbell,  
337 Suraci, & Williams, 2017), while the drift and buoyancy inferred from time-depth recorders

338 can provide information on the foraging success of marine predators (Abrahms et al., 2018). A  
339 further refinement is provided by indirect parameters such as those obtained by means of  
340 sensors that detect stomach, oesophageal or visceral temperature, which can provide invaluable  
341 insights into actual prey captures (Weimerskirch, Gault, & Cherel, 2005; Weimerskirch,  
342 Pinaud, Pawlowski, & Bost, 2007; Wilson, Cooper, & Plötz, 1992). An intriguing alternative  
343 is based on attaching a Hall sensor to one mandible opposite a magnet attached on the other  
344 mandible (but the ethical implications and feasibility must be well considered). The inter-  
345 mandibular angle can be determined by measuring changes in magnetic field strength (Wilson,  
346 Steinfurth, Ropert-Coudert, Kato, & Murita, 2002). This approach, which has been employed  
347 in several marine and terrestrial species, can provide information about both the number of  
348 food items and the type of food ingested (Ropert-Coudert et al., 2004). Indeed, such is the detail  
349 provided by these sensors that studies are now able to examine food acquisition within a  
350 probabilistic framework and thereby make predictions about how food abundance may affect  
351 populations (Wilson, Neate, et al., 2018).

352

353 Obtaining direct observations may sometimes be essential, either because robust calibration of  
354 bio-logging sensors is difficult, or because the study's aim is to document particular behaviours  
355 in great detail (such as prey captures and social interactions; McInnes, McGeorge, Ginsberg,  
356 Pichegru, & Pistorius, 2017; Pagano et al., 2018; Watanabe & Takahashi, 2013) or to prospect  
357 for undiscovered behaviours (such as unusual foraging techniques; Rutz, Bluff, Weir, &  
358 Kacelnik, 2007). Under these circumstances, video loggers are the method of choice, or still-  
359 image loggers, if longer recording times are required and a lower frame rate is acceptable.  
360 Cameras may also offer the opportunity to assess what a wild animal sees in the field (Moll,  
361 Millspaugh, Beringer, Sartwell, & He, 2007) so that environmental information can be factored  
362 into foraging efficiency (Sutton, Hoskins, & Arnould, 2015) and movement patterns studied  
363 with respect to visual stimuli (Tremblay, Thibault, Mullers, & Pistorius, 2014). Video loggers  
364 can also be combined effectively with other sensors such as accelerometers (Watanabe &  
365 Takahashi, 2013), and are small enough to be fitted to a wide range of species (see below).

366

## 367 **2. From sensors to data**

368 Data collection and analysis issues must be addressed alongside sensor selection when  
369 approaching a specific ecological question. The first challenge concerns finding the most  
370 appropriate experimental/sampling design to answer a given ecological question. More broadly  
371 (see the internal data node of the IBF), this concerns the closely related issues of tag design,

372 data management (which includes planning for data archiving and sharing) – all of which must  
373 be defined prior to field work. The experimental design will strongly benefit from  
374 interdisciplinary collaborations to find the best solution, ensuring that the data-gathering is both  
375 feasible and will lead to sufficient data to answer the questions using available analytic  
376 techniques.

377

### 378 *2.1 Experimental design*

379 Consideration of an appropriate sampling regime prior to tag deployment, so as not to over-,  
380 or under-sample and maximise battery duration (and minimize tag weight), is a crucial aspect  
381 (note that battery power is required both to interrogate the sensors and write the data to  
382 memory, and possibly send the data). To do so, researchers should apply the Nyquist or  
383 sampling theorem, which states that the sampling frequency should be at least twice the fastest  
384 frequency of interest; e.g. consider wingbeat frequency vs. amplitude as focus of interest. This  
385 also holds true in temporal and spatial domains (see discussion in Ropert-Coudert & Wilson,  
386 2004). An obvious consequence of this trade-off is the use of smart sampling, whereby the  
387 sensors record at a frequency able to elucidate the relevant aspect properly, but no more. We  
388 do note, however, that highly prescribed, low frequency sampling may miss serendipitous  
389 observations of importance and may preclude the detection of new, never observed behaviours.  
390 Furthermore, derivation of body motion or measures of energy expenditure (DBA) requires  
391 smoothing of accelerometer data at an appropriate frequency (Shepard, Wilson, Halsey, et al.,  
392 2008), albeit the latter could indeed be processed on-board without storing the high frequency  
393 data (e.g. Cox et al., 2018). For example, a high frequency recording of raw data (> 20 Hz)  
394 may be necessary to compute animal posture and DBA (see also Brownscombe, Lennox,  
395 Danylchuk, & Cooke, 2018), however, higher frequencies draw more current, thus a balance  
396 between behaviour resolution, information gain, and current draw is a key stage of  
397 experimental design. An area of current research (e.g. see Cox et al., 2018) is focussing on  
398 finding clever ways to store on-board only sub-sampled or summary data, rather than the raw  
399 high-frequency data, thereby reducing data storage requirements and, ideally, allow remote  
400 transmission of the data (often the latter is precluded for field studies due to the high power  
401 requirement). Closely related is the choice of sensor resolution (bit resolution, see discussion  
402 and examples in Ropert-Coudert & Wilson, 2004). The number of bits with which the data are  
403 stored directly determines the quality of the data obtained. For example, past loggers used an  
404 8-bit resolution, meaning the sensor can obtain an absolute resolution given by the maximum  
405 resolution range divided by 256. In the case of a depth pressure transducer with a maximum

406 range of 50 Bar this means a maximum resolution of circa 0.2 Bar, equal to resolving dive  
407 differences of 2 m (a 16-bit resolution allows instead to resolve steps of 0.008 m, see Ropert-  
408 Coudert & Wilson, 2004). Low resolution may preclude recording key information such as  
409 prey capture events. Equally important is the measurement range of the sensor. For example,  
410 an accelerometer which records up to 8 g will miss any data of animals moving more  
411 dynamically (e.g. head impacts) and unless the animals are known to be only relatively slow  
412 moving and good preliminary data exist, researchers should set the range to at least 16 g for  
413 initial studies (for terrestrial systems; a lower range may be sufficient for aquatic systems as,  
414 due to friction, movement speed may change less fast), and record this information in the  
415 metadata. Equally important are trade-offs between the quantity of data collected and the time  
416 a tag collects data on an individual, as well as trade-offs between the amount of data collected  
417 on single individuals against the number of different animals monitored across time and space  
418 (see also Hebblewhite & Haydon, 2010). Collaborations across disciplines are crucial to make  
419 such decisions.

420

## 421 *2.2 Tag design*

422 Reducing battery consumption not only extends the life of a bio-logging device, but has  
423 implications for tag size and attachment that should also be considered for both optimal study  
424 design and animal welfare. Reduction of tag size is paramount, yet even with recent advances  
425 in the reduction of sensor size, it is still battery size that limits that of the device. For cameras  
426 for example, current available loggers are small enough, at approximately 10 g, to be fitted to  
427 a wide range of species (Rutz et al., 2007). However, even state-of-the-art camera loggers  
428 remain severely battery limited, hence duty cycling is advisable for most applications, as this  
429 allows targeted data collection during periods of peak activity and/or repeated short-term  
430 recording over the course of several days (Rutz & Troscianko, 2013). An exciting recent  
431 development is the use of event-triggering technology that allows cameras to be switched on  
432 whenever particular behavioural states or environmental conditions are detected (see analysis  
433 section below).

## 433 *2.3 Data management*

434 A further consideration for optimal experimental design is that of data management and  
435 processing. The data provided by sensors often do not correspond directly to the information  
436 we look for, but to a proxy, which needs to be converted. For instance, a depth recorder is  
437 designed to provide a measure of pressure rather than a measure of depth, but underwater depth  
438 being linearly related to pressure, the conversion is straightforward. For other sensors, this is  
439 not so obvious, and raw data therefore require being pre-processed. For example, acceleration

440 data do not provide a direct estimate of energy expenditure or oxygen consumed while moving.  
441 First, the dynamic component has to be extracted from the raw acceleration values, then  
442 converted to DBA, which finally has to be correlated with energy or oxygen through controlled  
443 lab experiments (reviewed in Wilson et al., accepted). Pre-processing is also required for  
444 integrating data provided by different sensors, possibly at different rates, and often based on  
445 separate clocks (exposing systems to clock drift); although inertial measurement units (IMUs)  
446 effectively deal with temporal synchronisation within any one logger. Notably, data recorded  
447 at high frequency are both noisy and highly serially auto-correlated. Noise can be reduced by  
448 filtering, e.g. by taking a running mean, or may involve more complex approaches such as  
449 Fourier transformations or Kalman filtering (e.g. Alam & Rohac, 2015). A simple and efficient  
450 solution consists of sub-sampling the processed data to a level (or deriving averages, see below)  
451 to accord with the Nyquist frequency. Pre-processing should be performed before subsampling,  
452 although there is an element of feedback depending on the desired end-point, which may also  
453 need to be considered when selecting the sampling frequencies for the different sensors and  
454 their data types, and also has important implications for data archiving (see next section).

455

#### 456 *2.4. Data archiving and sharing*

457

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

473

474

475 **3. From data to analysis**

476 Data analysis issues must be addressed upfront alongside sensor selection and experimental  
477 design, to ensure the resulting data are sufficient for the proposed mathematical models and  
478 statistical tests used to infer biological information from the data. This requires strong inter-  
479 disciplinary collaborations between empiricists and theoreticians from the outset of the project.  
480 The first major challenge for the link between data collection and analyses in the IBF is the  
481 ‘big data’ problem. Rapid advances in bio-logging technology now provide information-rich,  
482 big data sets, even from single individuals, thus the challenges in data analyses are similar to  
483 those of ‘big data’ and ‘data science’ problems in ecology and science (Hampton et al., 2013;  
484 Lewis, Vander Wal, & Fifield, 2018; Thums et al., 2018). There is an urgent need for the use  
485 and development of more sophisticated and computationally efficient data visualisation and  
486 exploration methods, as well as mathematical models that incorporate multidimensional bio-  
487 logging data.

488

489 *3.1 Data Visualisation*

490 A key part of exploratory data analysis consists in devising efficient ways to visualise and  
491 display quantitative information (Tukey, 1977). Data visualisation converts complex patterns  
492 in data into a visual display, capitalising on the extraordinary capacity of the human visual  
493 system to pick out patterns in complex landscapes, and thereby provide insights into data  
494 relations (Ware, 2012). While ecologists often develop their own visualisation tools, many  
495 methods come from other disciplines such as geographic information science (Demšar et al.,  
496 2015; Li, Wu, Song, & Zhou, 2016), medicine and neuroscience (with complex fMRI data e.g.  
497 de Ridder, Klein, & Kim, 2017).

498

499 Conventionally, acceleration data tend to be visualised as time series plots (Figure 4A), with  
500 analyses based on summary statistics (derived from ethograms; Figure 4B) and the application  
501 of data transformations. While such approaches are useful for classification of time series data  
502 (Walker et al., 2015), integration of multi-sensor data are poorly covered by this approach (Lee  
503 & Jeong, 2017; Li et al., 2016; Walker, Borgo, & Jones, 2016), primarily due to time taking up  
504 one axis and constraining all other data to lie within its scaling and bounds. Other visualisations  
505 may bypass the time scaling factor by having spherical plots that present 3-dimensional  
506 scatterplots, histograms, clustering data by behavioural state (Grundy, Jones, Laramée, Wilson,  
507 & Shepard, 2009; Williams et al., 2017; Wilson et al., 2016; Figures 4C-E). The value in these

508 spherical plots is that they are also multi-layer and present environmental data such as pressure  
509 and temperature as well as metrics of energetic expenditure (Roberts, Laramée, & Jones, 2015).  
510 In addition, time can also be represented, if necessary, by glyph or line colour (Figure 4E).  
511 Thus, such visual analytics systems can be linked interactively to allow different aspects of the  
512 same data to be explored, with and without temporal and spatial scales. In terms of sensor data  
513 this includes plots in tri-axial space with further dimensions related to movement and  
514 performance metrics (e.g. Roberts et al., 2015) and those that combine multi-dimensional  
515 trajectory visualisations on a map with environmental data (e.g. Buchin et al., 2015; Shamoun-  
516 Baranes et al., 2016; Figure 4F) and temporal visualisations (Demšar et al., 2015) such as  
517 DynamoVis (Dodge, Xavier, & Wong, 2018; Xavier & Dodge, 2014) or flow visual analytics  
518 systems (Andrienko, Andrienko, Chen, Maciejewski, & Zhao, 2017; Graser, Schmidt, Roth, &  
519 Brändle, 2017; Figure 4G). Time is also commonly visualised through animation and there are  
520 two R packages that support this (albeit for traditional location-only data, not logger data):  
521 moveVis (Schwalb-Willmann, 2018) and anipaths (Scharf, 2018). See supplementary  
522 information for a detailed list of current visualisations (SI Table 3). Current developments  
523 indicate that it may be possible to bring these multi-dimensional plots into an interactive 3-  
524 dimensional lab space beyond a digital screen, which would dramatically help exploration of  
525 data and even advance behavioural studies through the manipulation of the virtual world (see  
526 Stowers et al., 2017). Equally important will be the development of improved ways to display  
527 results from machine-learning methods (see below); again, an area for which multi-disciplinary  
528 collaborations will be crucial.

529

### 530 *3.2 Behavioural Classification*

531 Behavioural classification involves identifying particular behaviour-linked signals within  
532 complex datasets, such as accelerometer and magnetometer data. This may involve searching  
533 for behaviour-linked thresholds, such as an increase in pressure to indicate diving (Kooyman,  
534 1964) but more commonly will involve consideration of multiple data streams (Viviant, Trites,  
535 Rosen, Monestiez, & Guinet, 2010; Yoda et al., 2001), which makes the process more complex.  
536 For this reason, much emphasis has recently been placed on machine learning algorithms  
537 (including K-Nearest Neighbour [KNN], Support Vector Machines [SVMs], Classification and  
538 Regression Trees [CART], and Artificial Neural Networks [ANNs]) to classify behaviours  
539 automatically (Nathan et al., 2012). Supervised machine-learning models are trained with  
540 segments of data that have been manually labelled according to behaviour (Carroll, Slip,  
541 Jonsen, & Harcourt, 2014; Watanabe & Takahashi, 2013). The convenience of machine-



542 learning systems is that they require little specialist knowledge about the data streams from the  
543 researcher. Against this, there is a tendency to put all primary data streams as well as derived  
544 elements (such as DBA metrics) into the process. Because the machine does not know which  
545 data streams are most relevant at the outset, processing times can be prohibitively long. An  
546 approach that attempts to deal with this uses a Boolean framework and requires that the  
547 researchers have enough specialist knowledge to be able to pick out a sequence of features in  
548 behaviours (systematic variation and direction in data streams over defined time periods) to be  
549 able to define the behaviour in a series of key elements. These are then defined in an algorithm  
550 and the computer made to search for exactly those conditions to define the behaviour (Wilson,  
551 Holton, et al., 2018). The obvious downside to this approach is the level of expertise of the user  
552 and familiarity with the meaning of the data streams, which highlights the crucial role  
553 ecologists and biologists have to play in making sure analysis results remain biologically sound  
554 and relevant. On the other hand, bio-logging sensor data allow the discovery of behaviours  
555 never seen before in animals (Wilson et al., 2014), thus both exploratory and confirmatory  
556 analyses, as well as supervised and non-supervised data analysis methods will be equally  
557 important for ecologists (see also Leos-Barajas et al., 2017). Behaviour classification using  
558 logger data can also inform the usage of more traditional and limited GPS data to identify  
559 different behaviours in the latter (e.g. Browning et al., 2018).

560

### 561 *3.3 Movement analyses in the bio-logging era*

562 There is a long history of theoretical investigation into the reasons and rules underpinning  
563 animal movement (Nathan et al., 2008) including optimal foraging theory (Houston, Clark,  
564 McNamara, & Mangel, 1988; Pyke, 1984). However, historically, there have been inadequate  
565 data on the energetics and the details of movements to embrace optimality properly.  
566 Consequently, theoretical movement ecology has tended to focus on statistical descriptions of  
567 movement that are agnostic to the underlying life-history needs that govern movement  
568 decisions. Step-selection analysis, for example, examines environmental features that are  
569 correlated to movements from one location to the next (Avgar, Potts, Lewis, & Boyce, 2016;  
570 Fortin et al., 2005; Thurfjell, Ciuti, & Boyce, 2014). As another example, there are a variety of  
571 techniques that use movement to infer changes in behaviour, by observing how features such  
572 as speed, or tortuosity change over time (Hooten, Johnson, McClintock, & Morales, 2017).  
573 These are categorised under various names such as state-space models (Jonsen et al., 2013;  
574 Morales, Haydon, Frair, Holsinger, & Fryxell, 2004; Patterson, Thomas, Wilcox, Ovaskainen,  
575 & Matthiopoulos, 2008), hidden Markov models (Langrock et al., 2012; McClintock &

576 Michelot, 2018), continuous time models (reviewed in Patterson et al., 2017), and behavioural  
577 change-point analyses (Edelhoff, Signer, & Balkenhol, 2016; Gurarie, Andrews, & Laidre,  
578 2009). Similarly, there has been significant interest in inferring broad-scale movement patterns,  
579 such as home range, migratory or dispersal patterns, from squared displacement statistics  
580 (Börger & Fryxell, 2012). There is also a long history of mathematical models for inferring  
581 space-use patterns from general features of movement, such as advective and diffusive  
582 components (Moorcroft & Lewis, 2006; Moorcroft, Lewis, & Crabtree, 1999; Potts & Lewis,  
583 2014). All of these examples model movement in a descriptive fashion, where the biases and  
584 correlations (Benhamou, 2014; Codling, Plank, & Benhamou, 2008) represent hypothesised  
585 behavioural features of the movement path and the aspects of the movement that we either do  
586 not have direct knowledge of or are unable to test, as ‘random walks’, or ‘hidden states’.  
587 Incorporating high-resolution information from bio-logging studies can change this, as well as  
588 enable us to answer questions that link movement decisions to the life-history needs of animals.  
589

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

604  
605 For example, by modifying step selection analysis and similar techniques to incorporate the  
606 energetic costs and benefits derived from detailed bio-logging data (acceleration and heart rate  
607 loggers), we may be able to uncover the bio-energetic reasons behind animal movement  
608 choices, rather than simply describing landscape aspects that co-vary with animal movement.  
609 This would help us re-visit old questions about the optimality of foraging decisions, and give

610 important behavioural insights into animal decision-making at fine scales as they move through  
611 their energy landscape (Shepard et al., 2013). Quantifying the effects of the environment on  
612 movement costs in this way could help also derive a proxy of energy cost based on  
613 environmental conditions, to use with movement data without bio-logging information (e.g.  
614 Figure 3).

615

616 An interesting development in that direction is by Hooten, Scharf, & Morales (2018), who  
617 present a new approach to analyse movement data including explicit mechanistic links to  
618 physiological dynamics, to better model decision making and movement in heterogeneous  
619 environments. Notably, this approach can be extended to accommodate additional data such as  
620 those provided by bio-loggers. Similarly, state-space models and behavioural change-point  
621 analysis would be enhanced greatly by careful incorporation of data on acceleration or energy  
622 expenditure. Indeed, the behavioural states in these models are often “hidden” (as in “hidden  
623 Markov model”) but the sort of bio-logging data described in this review may be able to shed  
624 light on these states more directly. This will be a major change in the field and allow markedly  
625 improved and biologically relevant understanding to be obtained; compared to any of the even  
626 most sophisticated modelling approaches currently used.

627

628

#### 629 **4. Future developments for optimising the use of bio-logging**

630 So far, we have reviewed the current technologies and techniques available in the bio-logging  
631 toolbox, and how we may optimise their use to answer the big questions in ecology through  
632 collaborations within the IBF. Here we highlight potential key future developments, across all  
633 nodes of the IBF, which would markedly advance the fields of bio-logging and movement  
634 ecology.

635

##### 636 *New sensors: from speed measurement to skin-patches*

637 As speed is a key parameter of movement, there is an urgent need for reliable speed sensors  
638 without the disadvantages (such as fouling) or limits of propellers, flexible paddles, and Pitot  
639 tubes (cf. Shepard, Wilson, Liebsch, et al., 2008). Speed of movement exposes animals  
640 differentially to conditions and equates to (the square root of) power. New sensors need not be  
641 limited to external sampling systems either. Animal skin-associated ‘patches’ are being  
642 increasingly used in lab scenarios to look at physiological variables such as stress hormones  
643 and other chemicals (Lee, Bakh, Bisker, Brown, & Strano, 2016), something that would find

644 great resonance in wild animal studies. We see huge scope for cross-fostering between these  
645 fields, but there are substantial challenges as many of these applications, such as those  
646 developed for human studies (Nikita, 2014; Yang, 2014), require powerful readers that operate  
647 at close range, and tend to be severely battery limited. Finally, tags need to be able to drop off  
648 more routinely and be recovered reliably over large spatial scales, to obtain the large amount  
649 of recorded data. This may also save the animal the stress of being recaptured and having to  
650 carry the tags for longer than necessary, with all the tag detriment issues that this engenders.

651

652 *Improved ethical and animal welfare methodologies*

653 Although sensor technology is advancing rapidly, the ethics of bio-logging is still a major  
654 concern both in terms of fitting the device, which often requires capture, and the effects of  
655 carrying a bio-logger for the study subject. Advancing methodology in capture and  
656 consideration of stress by the animal is something that ecologists can work on. Be it reducing  
657 handling times, protecting a nest from predators or competitors while the animal is unable to,  
658 or even advancing remote tagging methods where the animal does not need to be handled. An  
659 additional limitation, is that most devices store data on-board, necessitating recapture of  
660 animals and the recovery of the units. Improving the ability of these devices to remotely  
661 transmit data would improve their applicability and reduce invasiveness, though may require  
662 additional weight in terms of electronics and battery. Of greater concern are tags which require  
663 surgical implantation. Recent advances have led to the development of surgically implanted  
664 sensors even measuring neurological activity, which may further our understanding of the  
665 mechanisms behind behaviour, but at what cost for the animal?

666

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

678 fluid dynamics to account for drag; Kay et al., accepted), considering also the often neglected  
679 effects of tag attachment itself (Vandenabeele et al., 2014). In the meantime, certainly  
680 researchers will have to better exploit the ongoing miniaturization to reduce the relative mass  
681 of the devices attached to animals (Portugal & White, 2018). Equally important, researchers  
682 should consider if a new tagging study is necessary, or if the question can be answered using  
683 existing published data or through data sharing, which will require the development of  
684 markedly improved data standards for bio-logging data (see previous section; Figure 3).

685

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

687 As bio-logging technology continues to advance, the ability to study an individual or  
688 population throughout their entire life from conception to death becomes a more realistic  
689 possibility. Such large-scale tagging has major ethical implications, as not only a small subset  
690 is affected but an entire group, community or population. Especially for similar large-scale  
691 questions, researchers would benefit from enhanced bandwidth for transmitting data (cf.  
692 O'Donoghue & Rutz, 2016), an element that is already being trialled within the ICARUS  
693 system (Wikelski et al., 2007). In tandem with this comes smart on-board data-processing (e.g.  
694 Cox et al., 2018) which has the potential to markedly increase the temporal and taxonomic  
695 range of data which can be collected. The combination therein of real-time processing and  
696 transmission of data will not only enable scientists to dynamically adapt experiments, but has  
697 applications in conservation and management.

698

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

700 Perhaps the most exciting aspect of bio-logging is that the data-rich approach driven by animals  
701 will not only help us to understand why animals do what they do, pinpointing drivers that range  
702 from internal state responses to pan-ocean basin atmospheric conditions, but thanks to an  
703 improved mechanistic understanding, we might actually be able to predict animal responses to  
704 future conditions. To do so will require a large improvement in the theoretical and  
705 mathematical foundations of movement ecology, to include the rich set of high-frequency  
706 multivariate data, which greatly expand the fundamentally limited and coarse data that could  
707 be collected using location-only technology such as GPS. In particular, there is a clear synergy  
708 between local (small-scale) information provided by sensors and large-scale information  
709 provided by, for example, remote sensing data. How to link and predict processes occurring  
710 across different scales is a central question in ecology (Levin, 1992) yet difficult to address,  
711 with the key issues being to identify the correct mesoscopic scale connecting microscopic

712 processes to macroscopic patterns. This is the case even for ‘simple’ physical systems  
713 constituted of identical particles, whereas biological systems are instead fundamentally  
714 characterised by additional intra- and inter-specific heterogeneity. Movement ecologists  
715 therefore have to deal with processes which span multiple scales of spatio-temporal and  
716 biological complexity (Torney, Hopcraft, Morrison, Couzin, & Levin, 2018). Hence,  
717 demanding yet exciting challenges lie ahead for integrating novel bio-logging data with  
718 ecological questions. We may now have access to vastly improved information for wild animal  
719 biologists to predict processes.

720

### 721 *Improved multi-disciplinary collaborations*

722 Collaboration is key to the framework’s success as a tool for optimisation of bio-logging  
723 studies. At the same time, ecologists can feed new developments back to other disciplines, e.g.  
724 as inspiration for new theorems (Cohen, 2004; Sturmfels, 2005), or for biologically inspired  
725 engineering (Bionics), such as new models of navigation inspired by ants (Esterley, McCreery,  
726 & Nagpal, 2017) or improved collective decision making in robot swarms (Ebert, Gauci, &  
727 Nagpal, 2018). Indeed, actions to bring together multi-disciplinary groups of experts are  
728 gathering momentum in movement ecology; these include the EU COST actions from MOVE  
729 to develop improved methods for knowledge discovery from moving objects and big data  
730 ([www.cost.eu/COST\\_Actions/ict/IC0903](http://www.cost.eu/COST_Actions/ict/IC0903)) with similar initiatives in the European Network for  
731 Radar Surveillance of Animal Movement (<http://www.enram.eu/>), the Special Interest Group  
732 in Movement Ecology of the British Ecological Society  
733 ([www.britishecologicalsociety.org/membership-community/special-interest-](http://www.britishecologicalsociety.org/membership-community/special-interest-groups/movement-ecology/)  
734 [groups/movement-ecology/](http://www.britishecologicalsociety.org/membership-community/special-interest-groups/movement-ecology/)) and the International Bio-Logging Society ([www.bio-](http://www.bio-logging.net/)  
735 [logging.net/](http://www.bio-logging.net/)).

736

737

### 738 **Conclusion**

739 We have i) reviewed how to optimise the use of bio-logging techniques for ecologists to be  
740 able to take full advantage of the paradigm-changing opportunities of bio-logging sensors for  
741 ecological research and ii) synthesised this into an Integrated Bio-logging Framework (IBF)  
742 for movement ecology research. We highlighted the many new and often unexplored  
743 opportunities to address biological questions using the most appropriate sensors and sensor-  
744 combinations, especially using multi-sensor approaches, a new frontier in bio-logging research.  
745 Given the technological complexities and rapid pace of advancement of the field, however,

746 establishing multi-disciplinary collaborations will be paramount for ecologists – and at the  
747 same time the latter can thereby more efficiently guide future technological and methodological  
748 advancements to address biological questions. Closely linked to the issue of matching  
749 ecological questions with sensors, is devising a good experimental design up front. This  
750 involves multiple closely connected challenges, from tag design and sampling regime, to the  
751 important related ethical and animal welfare considerations, and the challenges of data sharing.  
752 Linking new bio-logging data types to the most adequate analytical techniques presents many  
753 new and often unsolved issues in particular, and will require multi-disciplinary collaborations  
754 to tackle the ‘big data’ problem, and improve the theoretical and mathematical foundations of  
755 movement ecology. The tasks ahead are challenging, but a clear potential exists for a vastly  
756 improved mechanistic understanding of animal movements and their role in ecological  
757 processes, from which we can build unprecedented and realistic predictive models.

758

759

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774

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776 The manuscript was conceived by LB in discussion with all authors at BES Move 2018. All  
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778 declare no conflicts of interest.

779

780 **Tables and Figures**

781

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

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

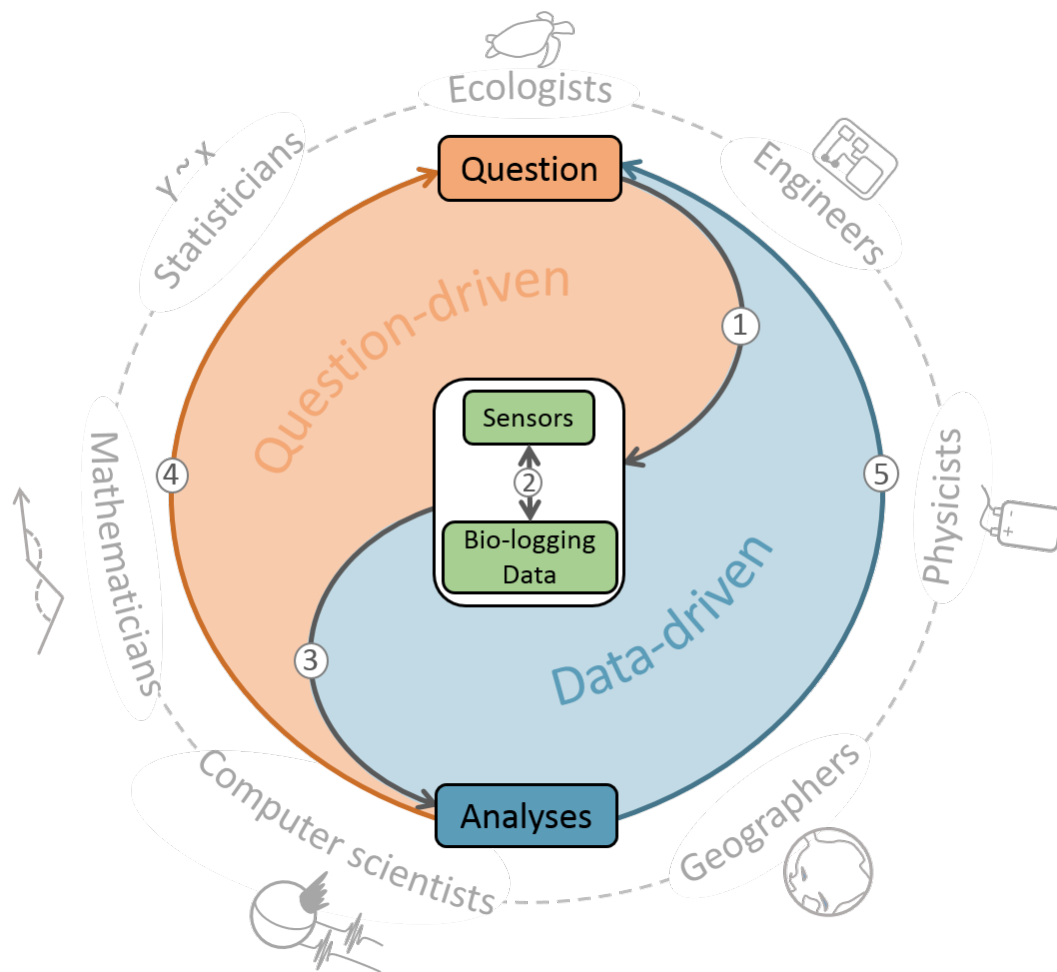
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Sensor type	examples	description	Relevant questions	optimisation
Location	Animal-borne radar, pressure, passive acoustic telemetry, proximity sensors	Location based on receiver location	Space use; interactions;	Use in combination with the behavioural 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 limb movement and vocal behaviour.		
Environment	Temperature	Ambient	Space use, energy expenditure; external factors; interactions	In situ remote sensing; arrays to localize animals; visualisations to provide context and understanding of interactions
	Microphone, proximity sensors, video loggers	Record external environment e.g. soundscape		

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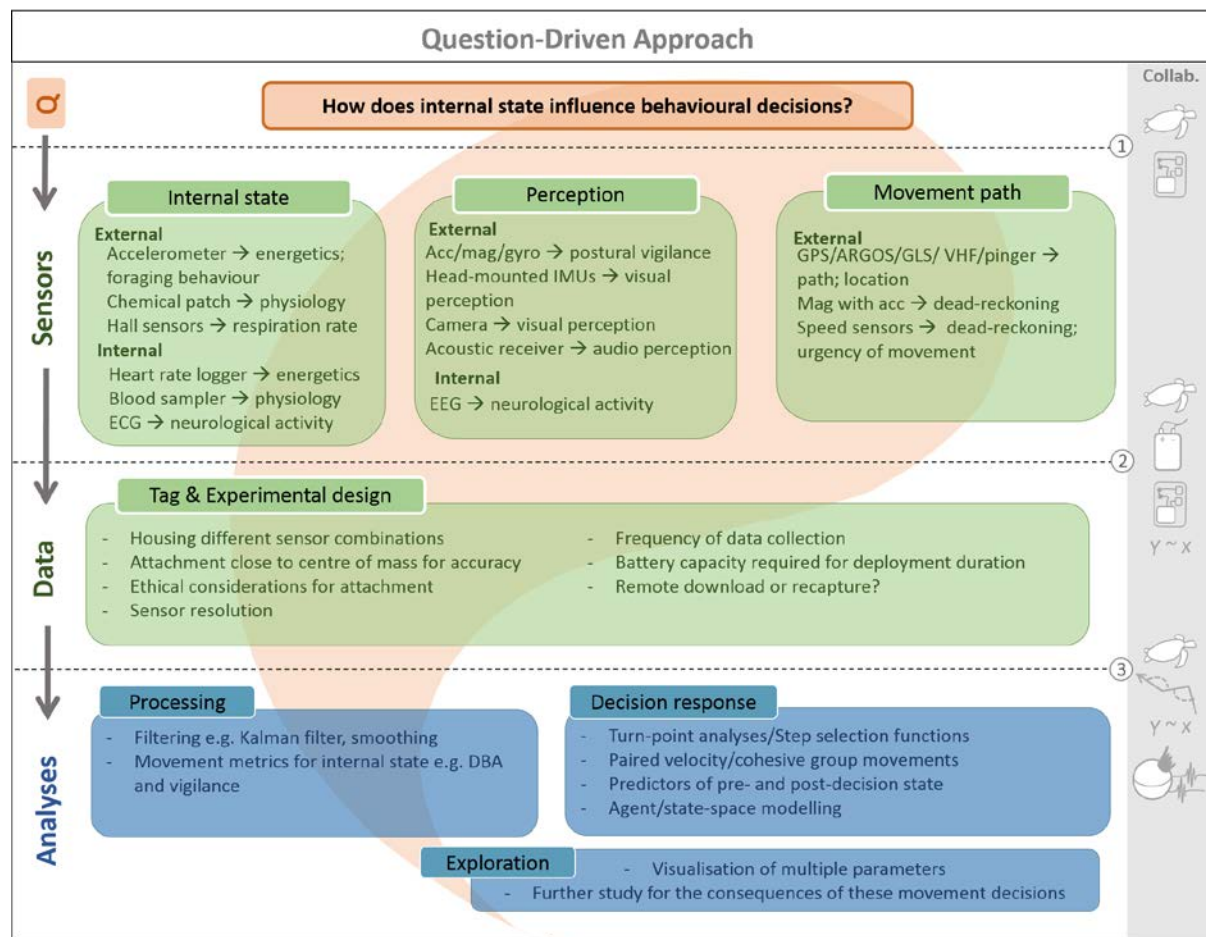




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788

789 Figure 1: *The Integrated Bio-logging Framework (IBF) for optimal use of bio-logging in*  
 790 *movement ecology*. Researchers may take a question-driven approach, beginning with a  
 791 *hypothesis*, then selecting the appropriate sensor and analysis techniques. Alternatively, a  
 792 *data-driven approach* can be taken, by allowing existing data to inform further hypotheses and  
 793 *data collection*. The framework operates via collaboration between disciplines in a system of  
 794 *feedback loops*, numbered as 1-5, though these collaborative links are not exclusive to any  
 795 *particular node*. Figures 2 and 3 provide illustrated examples for the use of the IBF.

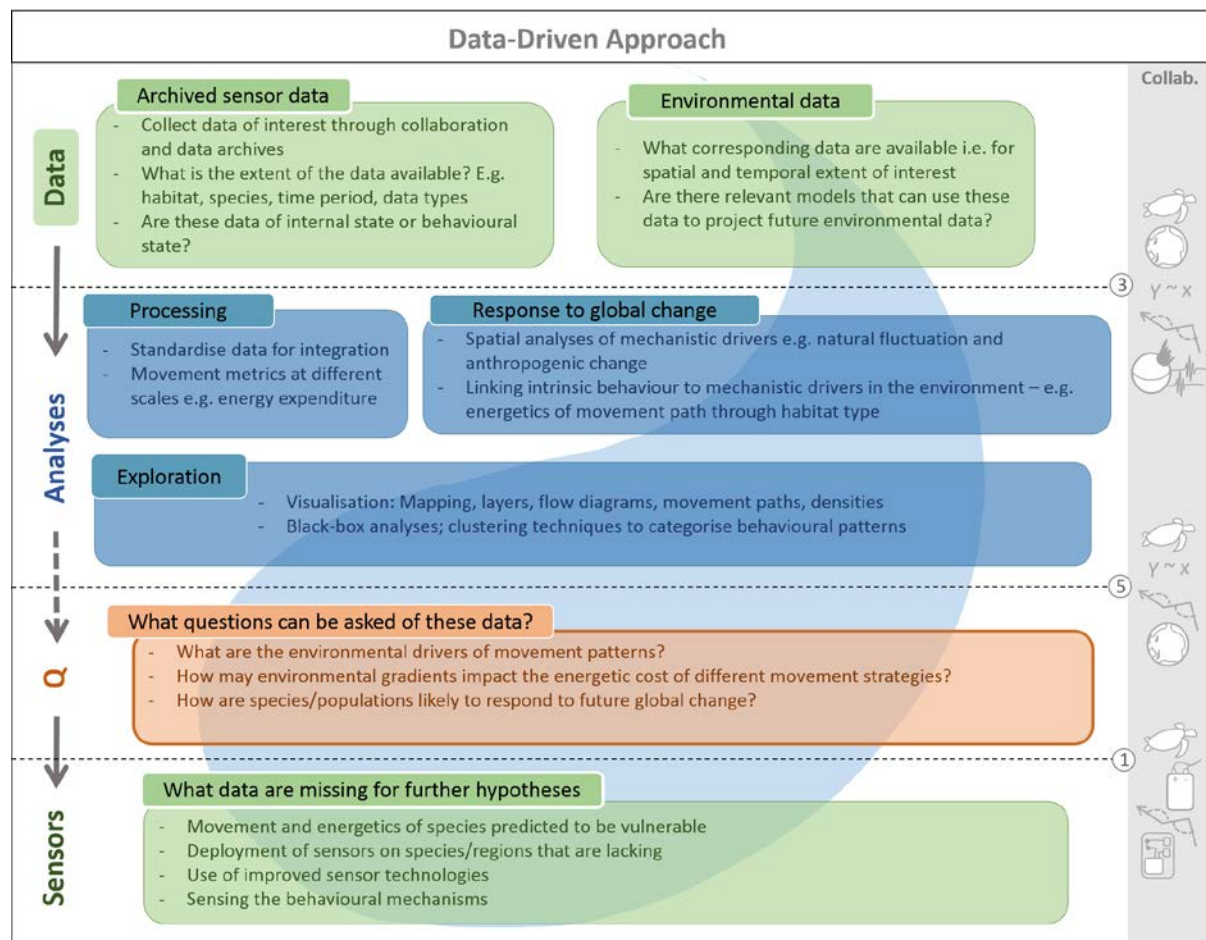


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797

798 **Figure 2: A question-driven approach to the IBF for optimal study design using bio-logging.**

799 *In this example, ecologists begin with their question of focus (top of Figure 1), in this case an*  
 800 *investigation into the effect of internal state on movement decisions, and select the appropriate*  
 801 *external and internal sensors for data collection. Here, sensors should be sensitive to different*  
 802 *aspects of an animal’s movement that relate to their internal state, perceived information and*  
 803 *the movement that may result from a particular decision. Selection of the sensors requires*  
 804 *strong collaboration between ecologists and engineers (right-hand symbols). Simultaneously*  
 805 *(bottom of Figure 1), ecologists should work with those analysing the data (e.g. physicists,*  
 806 *mathematicians, statisticians, computer scientists) in the process of designing the data*  
 807 *collection, to ensure the correct data are gathered that can answer the question using the*  
 808 *analytic tools available.*



**Collab.**

3

$Y \sim X$

5

$Y \sim X$

1

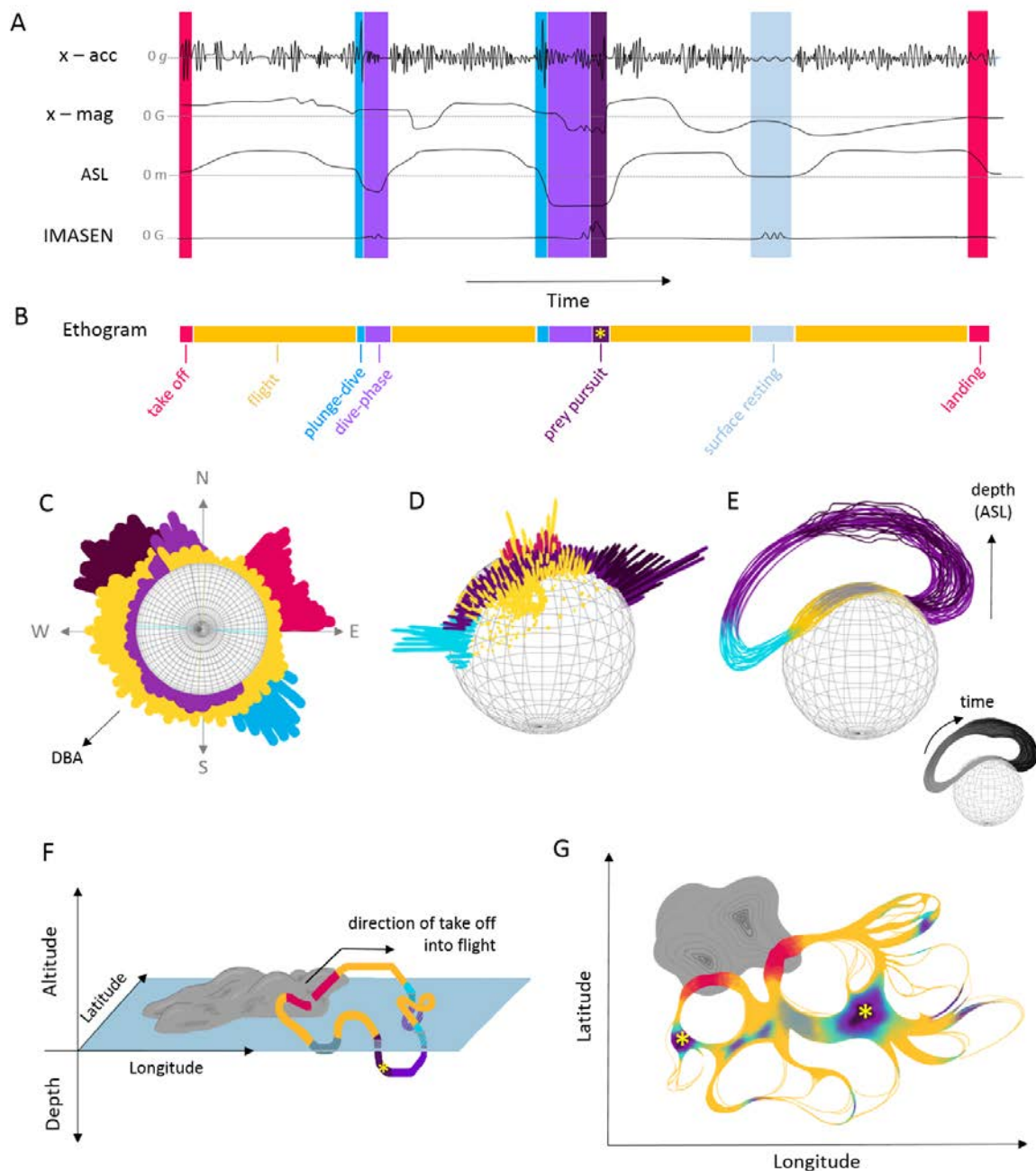
**What data are missing for further hypotheses**

- Movement and energetics of species predicted to be vulnerable
- Deployment of sensors on species/regions that are lacking
- Use of improved sensor technologies
- Sensing the behavioural mechanisms

809

810

811 Figure 3: A **data-driven approach to the IBF for optimal study design using archived bio-**  
 812 **logging data.** In this example, ecologists begin by selecting appropriate data types for the study  
 813 of movement patterns in relation to environmental measures at local and global scales.  
 814 Understanding and predicting how animals respond to global change, including climate and  
 815 land-use change, requires multiple data collected over a range of temporal and spatial scales.  
 816 In this case, ecologists start at the central nodes of the IBF (Figure 1) to collate archived data  
 817 and collaborate with mathematicians, statisticians and geographers (right-hand symbols) to  
 818 implement the appropriate processing and analytical techniques to interrogate the data and  
 819 identify patterns by which several questions may be approached. Following this, ecologists  
 820 may work with other disciplines to deploy additional bio-logging sensors to collect data that  
 821 complement the shared data.



822

823 Figure 4: **Visualisation of sensor and location data.** A number of schematic plots of varying  
 824 axes and information types to visualise data of a seabird in flight that plunge-dives in pursuit  
 825 of prey. A) Logged sensor outputs (acceleration (g), magnetometry ( $\mu$ T), altitude above sea  
 826 level (m) derived from pressure data (kPa) and the inter-mandibular angle sensor IMASEN  
 827 output ( $\mu$ T)) in a time series plot. Peaks in dynamic acceleration are associated with wing  
 828 beats during take-off (red) and in flight (yellow), as well on impact with the sea surface in  
 829 plunge-dives (aqua blue). During the dive, as indicated by the negative altitude above sea level  
 830 (ASL; purple) the bird may pursue prey (dark purple), as indicated by increased variation in

831 *acceleration and heading, from the magnetometer output. A successful prey capture attempt is*  
832 *evident in the peaks in the IMASEN signal output, as the bird opens its bill to capture the prey*  
833 *(yellow asterisk). B) The behaviours are classified and presented in an ethogram to show*  
834 *temporal variation in behaviour (this serves as a key for the schematic). Further to these time*  
835 *series plots, different sensor outputs can be combined, along with derived metrics, in various*  
836 *multi-axes visualisations to reveal patterns in behaviour. We present three examples (C-E) for*  
837 *data visualisation in multi-dimensional space and two for geographic space (F-G): C) a*  
838 *circular plot of heading on an m-sphere (magnetometry; Williams et al., 2017), where height*  
839 *of the bar is the magnitude of the extent of movement (DBA), the most active behaviours for*  
840 *this bird are foraging and diving, which occur at opposite headings; D) a g-sphere (static*  
841 *acceleration data) or Dubai plot, where a frequency histogram of static acceleration is*  
842 *resolved in tri-axial space (Wilson et al., 2016) and peaks show the most common postures for*  
843 *each behaviour; E) a g-sphere where distance from the surface of the sphere is relative to the*  
844 *depth below sea level, where colour indicates different behaviours in the dive, so that through*  
845 *the dive there is a shift in posture, and a greater variation in posture and depth during the prey*  
846 *pursuit (coloured by time in greyscale, bottom right); F) 3D movement path during for the*  
847 *foraging trip; G) 2D flow visualisation of foraging path, where thicker paths are more*  
848 *commonly used for the different behaviours (Verbeek, Buchin, & Speckmann, 2011).*

849 **References**

850

851 Abrahms, B., Scales, K. L., Hazen, E. L., Bograd, S. J., Schick, R. S., Robinson, P. W., &  
852 Costa, D. P. (2018). Mesoscale activity facilitates energy gain in a top predator.  
853 *Proceedings of the Royal Society B: Biological Sciences*, 285, 20181101.  
854 doi:10.1098/rspb.2018.1101

855 Alam, M., & Rohac, J. (2015). Adaptive data filtering of inertial sensors with variable  
856 bandwidth. *Sensors*, 15(2), 3282–3298. doi:10.3390/s150203282

857 Andrienko, G., Andrienko, N., Chen, W., Maciejewski, R., & Zhao, Y. (2017). Visual analytics  
858 of mobility and transportation: State of the art and further research directions. *IEEE*  
859 *Transactions on Intelligent Transportation Systems*, 18(8), 2232–2249.  
860 doi:10.1109/TITS.2017.2683539

861 Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis:  
862 Bridging the gap between resource selection and animal movement. *Methods in Ecology*  
863 *and Evolution*, 7(5), 619–630. doi:10.1111/2041-210X.12528

864 Barron, D. G., Brawn, J. D., & Weatherhead, P. J. (2010). Meta-analysis of transmitter effects  
865 on avian behaviour and ecology. *Methods in Ecology and Evolution*, 1(2), 180–187.  
866 doi:10.1111/j.2041-210X.2010.00013.x

867 Benhamou, S. (2014). Path integration and coordinate systems. *Journal of Theoretical Biology*,  
868 349, 163–166. doi:10.1016/j.jtbi.2014.02.012

869 Benhamou, S. (2018). Mean squared displacement and sinuosity of three-dimensional random  
870 search movements. *ArXiv*, 1801.02435. Retrieved from <http://arxiv.org/abs/1801.02435>

871 Bettaney, E. M., James, R., St Clair, J. J. H., & Rutz, C. (2015). Processing and visualising  
872 association data from animal-borne proximity loggers. *Animal Biotelemetry*, 3, 27.  
873 doi:10.1186/s40317-015-0065-4

874 Bidder, O. R., Qasem, L. A., & Wilson, R. P. (2012). On higher ground: how well can dynamic  
875 body acceleration determine speed in variable terrain? *PLoS ONE*, 7(11), e50556.  
876 doi:doi:10.1371/journal.pone.0050556

877 Bidder, O. R., Walker, J. S., Jones, M. W., Holton, M. D., Urge, P., Scantlebury, D. M., ...  
878 Wilson, R. P. (2015). Step-by-step: reconstruction of terrestrial animal movement paths  
879 by dead-reckoning. *Movement Ecology*, 3, 23. doi:0.1186/s40462-015-0055-4

880 Biewener, A. A., & Patek, S. N. (2018). *Animal locomotion* (2nd ed.). Oxford, UK: Oxford  
881 University Press.

882 Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., ... Butler,



- 883 P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during  
884 Himalayan migrations. *Science*, 347(6219), 250–254. doi:10.1126/science.1258732
- 885 Block, B. A. (2005). Physiological Ecology in the 21st Century: Advancements in Biologging  
886 Science. *Integrative and Comparative Biology*, 45(2), 305–320.  
887 doi:https://doi.org/10.1093/icb/45.2.305
- 888 Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & Bearhop, S. (2018).  
889 A phylogenetically controlled meta-analysis of biologging device effects on birds:  
890 Deleterious effects and a call for more standardized reporting of study data. *Methods in*  
891 *Ecology and Evolution*, 9(4), 946–955. doi:10.1111/2041-210X.12934
- 892 Börger, L., & Fryxell, J. (2012). Quantifying individual differences in dispersal using net  
893 squared displacement. In J. Clobert, M. Baguette, T. G. Benton, & J. M. Bullock (Eds.),  
894 *Dispersal Ecology and Evolution* (pp. 222–230). Oxford, UK: Oxford University Press.
- 895 Bramanti, M., & Dall’Antonia, L. (1988). A new technique to monitor the flight paths of birds.  
896 *Journal of Experimental Biology*, 134, 467–472.
- 897 Browning, E., Bolton, M., Owen, E., Shoji, A., Guilford, T., & Freeman, R. (2018). Predicting  
898 animal behaviour using deep learning: GPS data alone accurately predict diving in  
899 seabirds. *Methods in Ecology and Evolution*, 9(3), 681–692. doi:10.1111/2041-  
900 210X.12926
- 901 Brownscombe, J. W., Lennox, R. J., Danylchuk, A. J., & Cooke, S. J. (2018). Estimating fish  
902 swimming metrics and metabolic rates with accelerometers: the influence of sampling  
903 frequency. *Journal of Fish Biology*, 93(2), 207–214. doi:10.1111/jfb.13652
- 904 Buchin, K., Sijben, S., van Loon, E. E., Sapir, N., Mercier, S., Arseneau, T. J. M., & Willems,  
905 E. P. (2015). Deriving movement properties and the effect of the environment from the  
906 Brownian bridge movement model in monkeys and birds. *Movement Ecology*, 3, 18.  
907 doi:10.1186/s40462-015-0043-8
- 908 Campbell, H. A., Urbano, F., Davidson, S., Dettki, H., & Cagnacci, F. (2016). A plea for  
909 standards in reporting data collected by animal-borne electronic devices. *Animal*  
910 *Biotelemetry*, 4, 1. doi:10.1186/s40317-015-0096-x
- 911 Carroll, G., Slip, D., Jonsen, I., & Harcourt, R. (2014). Supervised accelerometry analysis can  
912 identify prey capture by penguins at sea. *Journal of Experimental Biology*, 217(24), 4295–  
913 4302. doi:10.1242/jeb.113076
- 914 Codling, E. A., Plank, M. J., & Benhamou, S. (2008). Random walk models in biology. *Journal*  
915 *of the Royal Society Interface*, 5(25), 813–834. doi:10.1098/rsif.2008.0014
- 916 Cohen, J. E. (2004). Mathematics Is Biology’s Next Microscope, Only Better; Biology Is

- 917 Mathematics' Next Physics, Only Better. *PLoS ONE*, 2(12), e439.  
918 doi:doi:10.1371/journal.pbio.0020439
- 919 Cooke, S. J., Nguyen, V. M., Kessel, S. T., Hussey, N. E., Young, N., & Ford, A. T. (2017).  
920 Troubling issues at the frontier of animal tracking for conservation and management.  
921 *Conservation Biology*, 31(5), 1205–1207. doi:10.1111/cobi.12895
- 922 Cox, S. L., Orgeret, F., Gesta, M., Rodde, C., Heizer, I., Weimerskirch, H., & Guinet, C.  
923 (2018). Processing of acceleration and dive data on-board satellite relay tags to investigate  
924 diving and foraging behaviour in free-ranging marine predators. *Methods in Ecology and*  
925 *Evolution*, 9(1), 64–77. doi:10.1111/2041-210X.12845
- 926 de Ridder, M., Klein, K., & Kim, J. (2017). Temporaltracks: visual analytics or exploration of  
927 4D fMRI time-series coactivation. In *Proceedings of the Computer Graphics*  
928 *International Conference (CGI '17)*. New York, USA. doi:10.1145/3095140.3095153
- 929 Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., ... Weibel,  
930 R. (2015). Analysis and visualisation of movement: an interdisciplinary review.  
931 *Movement Ecology*, 3, 5. doi:10.1186/s40462-015-0032-y
- 932 Dimiceli, V. E., Piltz, S. F., & Amburn, S. A. (2011). Estimation of Black Globe Temperature  
933 for Calculation of the Wet Bulb Globe Temperature Index. In *Proceedings of the World*  
934 *Congress on Engineering and Computer Science 2011* (Vol. II, p. WCECS 2011, October  
935 19-21, 2011, San Francisco, US).
- 936 Ditmer, M. A., Rettler, S. J., Fieberg, J. R., Iaizzo, P. A., Laske, T. G., Noyce, K. V., &  
937 Garshelis, D. L. (2018). American black bears perceive the risks of crossing roads.  
938 *Behavioral Ecology*, 29(3), 667–675. doi:10.1093/beheco/ary020
- 939 Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., ... Wikelski, M.  
940 (2013). The environmental-data automated track annotation (Env - DATA) system:  
941 linking animal tracks with environmental data. *Movement Ecology*, 1, 3.  
942 doi:10.1186/2051-3933-1-3
- 943 Dodge, S., Xavier, G., & Wong, W. Y. (2018). DynamoVis - Dynamic Visualization of Animal  
944 Movement Data. Retrieved from the Data Repository for the University of Minnesota.  
945 doi:10.13020/D6PH49
- 946 Downey, L. A., Tysse, B., Ford, T. C., Samuels, A. C., Wilson, R. P., & Parrott, A. C. (2017).  
947 Psychomotor Tremor and Proprioceptive Control Problems in Current and Former  
948 Stimulant Drug Users: An Accelerometer Study of Heavy Users of Amphetamine,  
949 MDMA, and Other Recreational Stimulants. *Journal of Clinical Pharmacology*, 57(10),  
950 1330–1337. doi:10.1002/jcph.925



- 951 Duda, N., Nowak, T., Hartmann, M., Schadhauer, M., Cassens, B., Wagemann, P., ... Kölpin,  
952 A. (2018). BATS: Adaptive Ultra Low Power Sensor Network for Animal Tracking.  
953 *Sensors*, 18(10), 3343. doi:10.3390/s18103343
- 954 Dunn, T. W., Mu, Y., Narayan, S., Radlett, O., Naumann, E. A., Yang, C.-T., ... Ahrens, M.  
955 B. (2016). Brain-wide mapping of neural activity controlling zebrafish exploratory  
956 locomotion. *ELIFE*, 5, e12741. doi:10.7554/eLife.12741
- 957 Ebert, J., Gauci, M., & Nagpal, R. (2018). Multi-Feature Collective Decision Making in Robot  
958 Swarms. In *Proceedings of the 17th International Conference on Autonomous Agents and*  
959 *MultiAgent Systems* (pp. 1711–1719). Stockholm, Sweden.
- 960 Edelhoff, H., Signer, J., & Balkenhol, N. (2016). Path segmentation for beginners: an overview  
961 of current methods for detecting changes in animal movement patterns. *Movement*  
962 *Ecology*, 4, 21. doi:10.1186/s40462-016-0086-5
- 963 Esterley, E. E., McCreery, H., & Nagpal, R. (2017). Models of Adaptive Navigation, Inspired  
964 by Ant Cooperative Transport in the Presence of Obstacles. In *2017 IEEE Symposium*  
965 *Series on Computational Intelligence (SSCI)* (pp. 1–8). Honolulu, USA.  
966 doi:10.1109/SSCI.2017.8280899
- 967 Fieberg, J., & Börger, L. (2012). Could you please phrase “home range” as a question? *Journal*  
968 *of Mammalogy*, 93(4), 890–902. doi:10.1644/11-MAMM-S-172.1
- 969 Fortin, D., Beyer, H. ., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. . (2005). Wolves  
970 influence elk movements: Behavior shapes a trophic cascade in Yellowstone national  
971 park. *Ecology*, 86(5), 1320–1330. doi:10.1890/04-0953
- 972 Getz, W. M., & Saltz, D. (2008). A framework for generating and analyzing movement paths  
973 on ecological landscapes. *Proceedings of the National Academy of Sciences of the United*  
974 *States of America*, 105(49), 19066–19071. doi:10.1073/pnas.0801732105
- 975 Graser, A., Schmidt, J., Roth, F., & Brändle, N. (2017). Untangling origin-destination flows in  
976 geographic information systems. *Information Visualization*, 1(1), 153–172.  
977 doi:10.1177/1473871617738122
- 978 Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and  
979 recommendations. *Comparative Biochemistry and Physiology. Part A, Molecular &*  
980 *Integrative Physiology*, 158(3), 287–304. doi:10.1016/j.cbpa.2010.09.011
- 981 Grundy, E., Jones, M. W., Laramée, R. S., Wilson, R. P., & Shepard, E. L. C. (2009).  
982 Visualisation of sensor data from animal movement. *Computer Graphics Forum*, 28(3),  
983 815–822. doi:10.1111/j.1467-8659.2009.01469.x
- 984 Gurarie, E., Andrews, R. D., & Laidre, K. L. (2009). A novel method for identifying

- 985 behavioural changes in animal movement data. *Ecology Letters*, 12(5), 395–408.  
986 doi:10.1111/j.1461-0248.2009.01293.x
- 987 Hall, E. H. (1879). On a New Action of the Magnet on Electric Currents. *American Journal of*  
988 *Mathematics*, 2(3), 287–292.
- 989 Hampton, S. E., Strasser, C. A., Tewksbury, J. J., Gram, W. K., Budden, A. E., Batcheller, A.  
990 L., ... Porter, J. H. (2013). Big data and the future of ecology. *Frontiers in Ecology and*  
991 *the Environment*, 11(3), 156–162. doi:10.1890/120103
- 992 Hays, G. C., Marshall, G. J., & Seminoff, J. A. (2007). Flipper beat frequency and amplitude  
993 changes in diving green turtles, *Chelonia mydas*. *Marine Biology*, 150(5), 1003–1009.  
994 doi:10.1007/s00227-006-0412-3
- 995 Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical  
996 review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the*  
997 *Royal Society B: Biological Sciences*, 365(1550), 2303–2312.  
998 doi:10.1098/rstb.2010.0087
- 999 Hedenström, A., Norevik, G., Warfvinge, K., Andersson, A., Bäckman, J., & Åkesson, S.  
1000 (2016). Annual 10-Month Aerial Life Phase in the Common Swift *Apus apus*. *Current*  
1001 *Biology*, 26(22), 3066–3070. doi:10.1016/j.cub.2016.09.014
- 1002 Hoenner, X., Huveneers, C., Steckenreuter, A., Simpfendorfer, C., Tattersall, K., Jaine, F., ...  
1003 Harcourt, R. (2018). Data Descriptor: Australia's continental-scale acoustic tracking  
1004 database and its automated quality control process. *Scientific Data*, 5, 170206.  
1005 doi:10.1038/sdata.2017.206
- 1006 Hooker, S. K., Barychka, T., Jessopp, M. J., & Staniland, I. J.  
1007 (2015). Images as proximity sensors: the incidence of conspecific foraging in Antarctic  
1008 fur seals. *Animal Biotelemetry*, 3, 37. doi:10.1186/s40317-015-0083-2
- 1009 Hooten, M. B., Johnson, D. S., McClintock, B. T., & Morales, J. M. (2017). *Animal movement:*  
1010 *statistical models for telemetry data*. Boca Raton, USA: CRC Press.
- 1011 Hooten, M., Scharf, H., & Morales, J. (2018). Running on empty: Recharge dynamics from  
1012 animal movement data. *Ecology Letters*, 22(2), 377–389. doi:10.1111/ele.13198
- 1013 Houston, A., Clark, C., McNamara, J., & Mangel, M. (1988). Dynamic models in behavioural  
1014 and evolutionary ecology. *Nature*, 332(3), 29–34.
- 1015 Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., ...  
1016 Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the  
1017 underwater world. *Science*, 348(6240), 1255642. doi:10.1126/science.1255642
- 1018 Jonsen, I. D., Basson, M., Bestley, S., Bravington, M. V., Patterson, T. A., Pedersen, M. W., ...  
1019 Wotherspoon, S. J. (2013). Deep-Sea Research II State-space models for bio-loggers: A

- 1019 methodological road map. *Deep-Sea Research Part II*, 88–89, 34–46.  
1020 doi:10.1016/j.dsr2.2012.07.008
- 1021 Kay, W. P., Naumann, D. S., Bowen, H. J., Withers, S., Evans, B. J., Wilson, R. P., ... Börger,  
1022 L. (accepted). Minimising the impact of biologging devices: Using Computational Fluid  
1023 Dynamics for optimising tag design and positioning. *Methods in Ecology and Evolution*.  
1024 Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an  
1025 eye on life and planet. *Science*, 348(6240), aaa2478. doi:10.1126/science.aaa2478
- 1026 Kenward, R. E. (2001). *A Manual for Wildlife Radiotracking*. London, UK: Academic Press.
- 1027 Kooyman, G. L. (1964). Techniques used in measuring diving capacities of Weddel seals. *The*  
1028 *Polar Record*, 12(79), 391–394.
- 1029 Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., & Rutz, C. (2013). Reality  
1030 mining of animal social systems. *Trends in Ecology and Evolution*, 28(9), 541–551.  
1031 doi:10.1016/j.tree.2013.06.002
- 1032 Krebs, J. R., & Davies, N. B. (1978). *Behavioural ecology: an evolutionary approach*. Oxford,  
1033 UK: Blackwell Scientific.
- 1034 Kröschel, M., Reineking, B., Werwie, F., Wildi, F., & Storch, I. (2017). Remote monitoring of  
1035 vigilance behavior in large herbivores using acceleration data. *Animal Biotelemetry*, 5(1),  
1036 10. doi:10.1186/s40317-017-0125-z
- 1037 Landry, M. P., Kruss, S., Nelson, J. T., Bisker, G., Iverson, N. M., Reuel, N. F., & Strano, M.  
1038 S. (2014). Experimental Tools to Study Molecular Recognition within the Nanoparticle  
1039 Corona. *Sensors*, 14(9), 16193–16211. doi:10.3390/s140916196
- 1040 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012).  
1041 Flexible and practical modeling of animal telemetry data: hidden Markov models and  
1042 extensions. *Ecology*, 93(11), 2336–2342. doi:10.1890/11-2241.1Lee, J., & Jeong, B.-K.  
1043 (2017). Understanding sensor data with uncertainty using a visual representation. In *IEEE*  
1044 *7th Annual Computing and Communication Workshop and Conference (CCWC)* (pp. 1–  
1045 2). Las Vegas, USA. doi:10.1109/CCWC.2017.7868476
- 1046 Lee, M. A., Bakh, N., Bisker, G., Brown, E. N., & Strano, M. S. (2016). A Pharmacokinetic  
1047 Model of a Tissue Implantable Cortisol Sensor. *Advanced Healthcare Materials*, 5(23),  
1048 3004–3015. doi:10.1002/adhm.201600650
- 1049 Lee, M. A., Nguyen, F. T., Scott, K., Chan, N. Y. L., Bakh, N. A., Jones, K. K., ... Strano, M.  
1050 S. (2018). Implanted Nanosensors in Marine Organisms for Physiological Biologging:  
1051 Design, Feasibility, and Species Variability. *ACS Sensors*, 4(1), 32–43. research-article.  
1052 doi:10.1021/acssensors.8b00538

- 1053 Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y. Y.,  
1054 Murgatroyd, M., & Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data  
1055 using hidden Markov models. *Methods in Ecology and Evolution*, 8(2), 161–173.  
1056 doi:10.1111/2041-210X.12657
- 1057 Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6), 1943–1967.  
1058 doi:10.2307/1941447
- 1059 Lewis, K. P., Vander Wal, E., & Fifield, D. A. (2018). Wildlife biology, big data, and  
1060 reproducible research. *Wildlife Society Bulletin*, 42, 172–179. doi:doi:10.1002/wsb.847
- 1061 Li, W., Wu, S., Song, M., & Zhou, X. (2016). A scalable cyberinfrastructure solution to support  
1062 big data management and multivariate visualization of time-series sensor observation  
1063 data. *Earth Science Informatics*, 9(4), 449–464. doi:10.1007/s12145-016-0267-1
- 1064 McClintock, B. T. B. T., & Michelot, T. (2018). momentuHMM: R package for generalized  
1065 hidden Markov models of animal movement. *Methods in Ecology and Evolution*, 9(6),  
1066 1518–1530. doi:10.1111/2041-210X.12995
- 1067 McInnes, A. M., McGeorge, C., Ginsberg, S., Pichegru, L., & Pistorius, P. A. (2017). Group  
1068 foraging increases foraging efficiency in a piscivorous diver, the African penguin. *Royal  
1069 Society Open Science*, 4, 170918. doi:10.1098/rsos.170918
- 1070 McNamara, J. M., & Houston, A. I. (1986). The Common Currency for Behavioral Decisions.  
1071 *The American Naturalist*, 127(3), 358–378.
- 1072 Merkle, J. A., Fortin, D., & Morales, J. M. (2014). A memory-based foraging tactic reveals an  
1073 adaptive mechanism for restricted space use. *Ecology Letters*, 17(8), 924–931.  
1074 doi:10.1111/ele.12294
- 1075 Moll, R. J., Millspaugh, J. J., Beringer, J., Sartwell, J., & He, Z. (2007). A new ‘view’ of  
1076 ecology and conservation through animal-borne video systems. *Trends in Ecology and  
1077 Evolution*, 22(12), 660–668. doi:10.1016/j.tree.2007.09.007
- 1078 Moorcroft, P. R., & Lewis, M. A. (2006). *Mechanistic home range analysis*. Princeton, USA:  
1079 Princeton University Press.
- 1080 Moorcroft, P. R., Lewis, M. A., & Crabtree, R. L. (1999). Home range analysis using a  
1081 mechanistic home range model. *Ecology*, 80(5), 1656–1665. doi:10.1890/0012-  
1082 9658(1999)080[1656:HRAUAM]2.0.CO;2
- 1083 Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting  
1084 more out of relocation data: building movement models as mixtures of random walks.  
1085 *Ecology*, 85(9), 2436–2445. doi:10.1890/03-0269
- 1086 Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., ...

- 1087 Haydon, D. T. (2010). Building the bridge between animal movement and population  
1088 dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
1089 365(1550), 2289–2301. doi:10.1098/rstb.2010.0082
- 1090 Nassar, P. N., Jackson, A. C., & Carrier, D. R. (2001). Entraining the natural frequencies of  
1091 running and breathing in guinea fowl (*Numida meleagris*). *The Journal of Experimental*  
1092 *Biology*, 204(9), 1641–1651.
- 1093 Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E.  
1094 (2008). A movement ecology paradigm for unifying organismal movement research.  
1095 *Proceedings of the National Academy of Sciences of the United States of America*,  
1096 105(49), 19052–19059. doi:10.1073/pnas.0800375105
- 1097 Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012).  
1098 Using tri-axial acceleration data to identify behavioral modes of free-ranging animals:  
1099 general concepts and tools illustrated for griffon vultures. *The Journal of Experimental*  
1100 *Biology*, 215(6), 986–996. doi:10.1242/jeb.058602
- 1101 Nikita, K. S. (2014). *Handbook of Biomedical Telemetry*. Hoboken, USA: John Wiley & Sons,  
1102 Inc.
- 1103 Noda, T., Kawabata, Y., Arai, N., Mitamura, H., & Watanabe, S. (2014). Animal-mounted  
1104 gyroscope/accelerometer/magnetometer: In situ measurement of the movement  
1105 performance of fast-start behaviour in fish. *Journal of Experimental Marine Biology and*  
1106 *Ecology*, 451, 55–68. doi:10.1016/j.jembe.2013.10.031
- 1107 O'Donoghue, P., & Rutz, C. (2016). Real-time anti-poaching tags could help prevent imminent  
1108 species extinctions. *Journal of Applied Ecology*, 53(1), 5–10. doi:10.1111/1365-  
1109 2664.12452
- 1110 O'Mara, M. T., Wikelski, M., Voigt, C. C., Ter Maat, A., Pollock, H. S., Burness, G., ...  
1111 Dechmann, D. K. N. (2017). Cyclic bouts of extreme bradycardia counteract the high  
1112 metabolism of frugivorous bats. *ELIFE*, 6, e26686. doi:10.7554/eLife.26686
- 1113 Pagano, A. M., Durner, G. M., Rode, K. D., Atwood, T. C., Atkinson, S. N., Peacock, E., ...  
1114 Williams, T. M. (2018). High-energy, high-fat lifestyle challenges an Arctic apex  
1115 predator, the polar bear. *Science*, 359(6375), 568–572. doi:10.1126/science.aan8677
- 1116 Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017).  
1117 Statistical modelling of individual animal movement: an overview of key methods and a  
1118 discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101(4), 399–  
1119 438. doi:10.1007/s10182-017-0302-7
- 1120 Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-

- 1121 space models of individual animal movement. *Trends in Ecology and Evolution*, 23(2),  
1122 87–94. doi:10.1016/j.tree.2007.10.009
- 1123 Peters, D. P. C., Burruss, N. D., Rodriguez, L. L., McVey, D. S., Elias, E. H., Pelzel-  
1124 McCluskey, A. M., ... Vivoni, E. R. (2018). An Integrated View of Complex Landscapes:  
1125 A Big Data-Model Integration Approach to Transdisciplinary Science. *BioScience*, 68(9),  
1126 653–669. doi:10.1093/biosci/biy069
- 1127 Piersma, T., & Lindström, Å. (2004). Migrating shorebirds as integrative sentinels of global  
1128 environmental change. *Ibis*, 146(Suppl. 1), 61–69. doi:10.1111/j.1474-  
1129 919X.2004.00329.x
- 1130 Portugal, S. J., & White, C. R. (2018). Miniaturization of biologgers is not alleviating the 5%  
1131 rule. *Methods in Ecology and Evolution*, 9(7), 1662–1666. doi:10.1111/2041-210X.13013
- 1132 Potts, J. R., Börger, L., Scantlebury, D. M., Bennett, N. C., Alagaili, A., & Wilson, R. P. (2018).  
1133 Finding turning-points in ultra-high-resolution animal movement data. *Methods in*  
1134 *Ecology and Evolution*, 9(10), 2091–2101. doi:10.1111/2041-210X.13056
- 1135 Potts, J. R., & Lewis, M. A. (2014). How do animal territories form and change? Lessons from  
1136 20 years of mechanistic modelling. *Proceedings of the Royal Society B: Biological*  
1137 *Sciences*, 281(1784), 20140231. doi:10.1098/rspb.2014.0231
- 1138 Pyke, G. H. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology*  
1139 *and Systematics*, 15, 523–575.
- 1140 Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., ... Wilson,  
1141 R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure;  
1142 should we be summing values or calculating the vector? *PLoS ONE*, 7(2), e31187.  
1143 doi:10.1371/journal.pone.0031187
- 1144 Rattenborg, N. C., Voirin, B., Cruz, S. M., Tisdale, R., Dell’Omo, G., Lipp, H., ... Vyssotski,  
1145 A. L. (2016). Evidence that birds sleep in mid-flight. *Nature Communications*, 7, 12468.  
1146 doi:10.1038/ncomms12468
- 1147 Remelgado, R., Wegmann, M., & Safi, K. (2019). rsMove – An R package to bridge Remote  
1148 Sensing and Movement Ecology. *Methods in Ecology and Evolution*. doi:10.1111/2041-  
1149 210X.13199
- 1150 Rempel, R. S., Rodgers, A. R., & Abraham, K. F. (1995). Performance of a GPS Animal  
1151 Location System under Boreal Forest Canopy. *The Journal of Wildlife Management*,  
1152 59(3), 543–551.
- 1153 Roberts, R. C., Laramée, R. S., & Jones, M. W. (2015). Multivariate hybrid visualisation of  
1154 ornithological sensor data. In R. Borgo & C. Turkay (Eds.), *Proceedings of Computer*

- 1155 *Graphics and Visual Computing (CGVC) 2015* (pp. 1–6). Eurographics Association.  
1156 doi:10.2312/cgvc.20151233
- 1157 Ropert-Coudert, Y., Kato, A., Liebsch, N., Wilson, R. P., Müller, G., & Baubet, E. (2004).  
1158 Monitoring jaw movements: A cue to feeding activity. *Game and Wildlife Science*, 20(4),  
1159 1–19.
- 1160 Ropert-Coudert, Y., Sato, K., Kato, A., Charrassin, J.-B., Bost, C.-A., Le Maho, Y., & Naito,  
1161 Y. (2000). Preliminary investigations of prey pursuit and capture by king penguins at sea.  
1162 *Polar Bioscience*, 13, 101–112.
- 1163 Ropert-Coudert, Y., & Wilson, R. P. (2004). Subjectivity in bio-logging science: do logged  
1164 data mislead? *Memoirs of the National Institute of Polar Research: Special Issue*, 58, 23–  
1165 33.
- 1166 Rutz, C., Bluff, L. A., Weir, A. A. S., & Kacelnik, A. (2007). Video Cameras on Wild Birds.  
1167 *Science*, 318(5851), 765. doi:10.1126/science.1146788
- 1168 Rutz, C., Burns, Z. T., James, R., Ismar, S. M. H., Burt, J., Otis, B., ... St Clair, J. J. H. (2012).  
1169 Automated mapping of social networks in wild birds. *Current Biology*, 22(17), R669–  
1170 R671. doi:10.1016/j.cub.2012.06.037
- 1171 Rutz, C., & Hays, G. C. (2009). New frontiers in biologging science. *Biology Letters*, 5(3),  
1172 289–292. doi:10.1098/rsbl.2009.0089
- 1173 Rutz, C., & Troscianko, J. (2013). Programmable, miniature video-loggers for deployment on  
1174 wild birds and other wildlife. *Methods in Ecology and Evolution*, 4, 114–122.  
1175 doi:10.1111/2041-210x.12003
- 1176 Scacco, M., Flack, A., Duriez, O., Wikelski, M., & Safi, K. (2019). Static landscape features  
1177 predict uplift locations for soaring birds across Europe. *Royal Society Open Science*, 5,  
1178 181440. doi:10.1098/rsos.181440
- 1179 Scharf, H. (2018). anipaths: Animation of Observed Trajectories Using Spline-Based  
1180 Interpolation. R package version 0.9.6. <https://CRAN.R-project.org/package=anipaths>.
- 1181 Schmidt-Nielsen, K. (1972). Locomotion: Energy Cost of Swimming, Flying, and Running.  
1182 *Science*, 177(4045), 222–228. doi:10.1126/science.177.4045.222
- 1183 Schwalb-Willmann, J. (2018). moveVis: Movement Data Visualization. R package version  
1184 0.9.8. <https://CRAN.R-project.org/package=moveVis>.
- 1185 Shamoun-Baranes, J., Farnsworth, A., Aelterman, B., Alves, J. A., Azijn, K., Bernstein, G., ...  
1186 van Gasteren, H. (2016). Innovative visualizations shed light on avian nocturnal  
1187 migration. *PLoS ONE*, 11(8), e0160106. doi:10.1371/journal.pone.0160106
- 1188 Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Laich, A. G., Gleiss, A. C., ...

- 1189 Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration  
1190 data. *Aquatic Biology*, 4(3), 235–241. doi:10.3354/ab00104
- 1191 Shepard, E. L. C., Wilson, R. P., Liebsch, N., Quintana, F., Laich, A. G., & Lucke, K. (2008).  
1192 Flexible paddle sheds new light on speed: a novel method for the remote measurement of  
1193 swim speed in aquatic animals. *Endangered Species Research*, 4, 157–164.  
1194 doi:10.3354/esr00052
- 1195 Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., & Forman, D. W. (2009). Pushed  
1196 for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving  
1197 bird. *Proceedings of the Royal Society B: Biological Sciences*, 276(1670), 3149–3155.  
1198 doi:10.1098/rspb.2009.0683
- 1199 Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., ...  
1200 Macdonald, D. W. (2008). Identification of animal movement patterns using tri-axial  
1201 accelerometry. *Endangered Species Research*, 10(1), 47–60. doi:10.3354/esr00084
- 1202 Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A., & Vosper, S.  
1203 B. (2013). Energy Landscapes Shape Animal Movement Ecology. *The American*  
1204 *Naturalist*, 182(3), 298–312. doi:10.1086/671257
- 1205 Shipley, J. R., Kapoor, J., Dreelin, R. A., & Winkler, D. W. (2018). An open-source sensor-  
1206 logger for recording vertical movement in free-living organisms. *Methods in Ecology and*  
1207 *Evolution*, 9(3), 465–471. doi:10.1111/2041-210X.12893
- 1208 Skocek, O., Nöbauer, T., Weilguny, L., Traub, F. M., Xia, C. N., Molodtsov, M. I., ... Vaziri,  
1209 A. (2018). High-speed volumetric imaging of neuronal activity in freely moving rodents.  
1210 *Nature Methods*, 15, 429–432. doi:10.1038/s41592-018-0008-0
- 1211 St Clair, J. J. H., Burns, Z. T., Bettaney, E. M., Morrissey, M. B., Otis, B., Ryder, T. B., ...  
1212 Rutz, C. (2015). Experimental resource pulses influence social-network dynamics and the  
1213 potential for information flow in tool-using crows. *Nature Communications*, 6, 7197.  
1214 doi:10.1038/ncomms8197
- 1215 Stowers, J. R., Hofbauer, M., Bastien, R., Griessner, J., Higgins, P., Farooqui, S., ... Straw, A.  
1216 D. (2017). Virtual reality for freely moving animals. *Nature Methods*, 14(10), 995–1002.  
1217 doi:10.1038/nmeth.4399
- 1218 Sturmfels, B. (2005). Can biology lead to new theorems? *Annual Report of the Clay*  
1219 *Mathematics Institute*, 13–26.
- 1220 Sutton, G. J., Hoskins, A. J., & Arnould, J. P. Y. (2015). Benefits of Group Foraging Depend  
1221 on Prey Type in a Small Marine Predator, the Little Penguin. *PLoS ONE*, 10(12),  
1222 e0144297. doi:10.1371/journal.pone.0144297



- 1223 M. J., Trathan, P. N., & Croxall, J. P. (2004). Penguin-mounted cameras glimpse  
1224 underwater group behaviour. *Proceedings of the Royal Society B: Biological Sciences*,  
1225 271(Suppl\_5), S281–S282. doi:10.1098/rsbl.2004.0182
- 1226 Takei, Y., Suzuki, I., Wong, M. K. S., Milne, R., Moss, S., Sato, K., & Hall, A. (2016).  
1227 Development of an animal-borne blood sample collection device and its deployment for  
1228 the determination of cardiovascular and stress hormones in phocid seals. *American*  
1229 *Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 311(4),  
1230 R788–R796. doi:10.1152/ajpregu.00211.2016
- 1231 Taylor, G. K., Reynolds, K. V., & Thomas, A. L. R. (2016). Soaring energetics and glide  
1232 performance in a moving atmosphere. *Philosophical Transactions of the Royal Society of*  
1233 *London B: Biological Sciences*, 371(1704), 20150398. doi:10.1098/rstb.2015.0398
- 1234 Thums, M., Fernández-Gracia, J., Sequeira, A. M. M., Eguíluz, V. M., Duarte, C. M., &  
1235 Meekan, M. G. (2018). How Big Data Fast Tracked Human Mobility Research and the  
1236 Lessons for Animal Movement Ecology. *Frontiers in Marine Science*, 5, 21.  
1237 doi:10.3389/fmars.2018.00021
- 1238 Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in  
1239 ecology and conservation. *Movement Ecology*, 2, 4. doi:10.1186/2051-3933-2-4
- 1240 Tomkiewicz, S. M., Fuller, M. R., Kie, J. G., & Bates, K. K. (2010). Global positioning system  
1241 and associated technologies in animal behaviour and ecological research. *Philosophical*  
1242 *Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2163–2176.  
1243 doi:10.1098/rstb.2010.0090
- 1244 Torney, C. J., Hopcraft, J. G. C., Morrison, T. A., Couzin, I. D., & Levin, S. A. (2018). From  
1245 single steps to mass migration: The problem of scale in the movement ecology of the  
1246 Serengeti wildebeest. *Philosophical Transactions of the Royal Society B: Biological*  
1247 *Sciences*, 373(1746), 20170012. doi:10.1098/rstb.2017.0012
- 1248 Tremblay, Y., Thibault, A., Mullers, R., & Pistorius, P. (2014). Bird-Borne Video-Cameras  
1249 Show That Seabird Movement Patterns Relate to Previously Unrevealed Proximate  
1250 Environment, Not Prey. *PLoS ONE*, 9(2), e88424. doi:10.1371/journal.pone.0088424
- 1251 Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S.  
1252 C., ... Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial  
1253 mammalian movements. *Science*, 359(6374), 466–469. doi:10.1126/science.aam9712
- 1254 Tukey, J. W. (1977). *Exploratory Data Analysis*. New York: Addison-Wesley.
- 1255 van Dam, R. P., Ponganis, P. J., Ponganis, K. V., Levenson, D. H., & Marshall, G. (2002).

- 1256        Stroke frequencies of emperor penguins diving under sea ice. *The Journal of Experimental*  
1257        *Biology*, 205, 3769–3774.
- 1258        Vandenabeele, S. P., Grundy, E., Friswell, M. I., Grogan, A., Votier, S. C., & Wilson, R. P.  
1259        (2014). Excess baggage for birds: Inappropriate placement of tags on gannets changes  
1260        flight patterns. *PLoS ONE*, 9(3), e92657. doi:10.1371/journal.pone.0092657
- 1261        Vandenabeele, S. P., Shepard, E. L. C., Grémillet, D., Butler, P. J., Martin, G. R., & Wilson,  
1262        R. P. (2015). Are bio-telemetric devices a drag? Effects of external tags on the diving  
1263        behaviour of great cormorants. *Marine Ecology Progress Series*, 519, 239–249.  
1264        doi:10.3354/meps11058
- 1265        Verbeek, K., Buchin, K., & Speckmann, B. (2011). Flow Map Layout via Spiral Trees. *IEEE*  
1266        *Transactions on Visualization and Computer Graphics*, 17(12), 2536–2544.  
1267        doi:10.1109/TVCG.2011.202
- 1268        Viviant, M., Trites, A. W., Rosen, D. A. S., Monestiez, P., & Guinet, C. (2010). Prey capture  
1269        attempts can be detected in Steller sea lions and other marine predators using  
1270        accelerometers. *Polar Biology*, 33(5), 713–719. doi:10.1007/s00300-009-0750-y
- 1271        Vyssotski, A. L., Serkov, A. N., Itskov, P. M., Dell’Omo, G., Latanov, A. V., Wolfer, D. P., &  
1272        Lipp, H.-P. (2006). Miniature Neurologgers for Flying Pigeons: Multichannel EEG and  
1273        Action and Field Potentials in Combination With GPS Recording. *Journal of*  
1274        *Neurophysiology*, 95(2), 1263–1273. doi:10.1152/jn.00879.2005
- 1275        Walker, J., Borgo, R., & Jones, M. (2016). TimeNotes: A study on effective chart visualization  
1276        and interaction techniques for time-series data. *IEEE Transactions on Visualization and*  
1277        *Computer Graphics*, 22(1), 549–558. doi:10.1109/TVCG.2015.2467751
- 1278        Walker, J. S., Jones, M. W., Laramee, R. S., Bidder, O. R., Williams, H. J., Scott, R., ... Wilson,  
1279        R. P. (2015). TimeClassifier: a visual analytic system for the classification of multi-  
1280        dimensional time series data. *The Visual Computer*, 31(6), 1067–1078.  
1281        doi:10.1007/s00371-015-1112-0
- 1282        Ware, C. (2012). *Information Visualization: Perception for Design* (3rd ed.). San Francisco,  
1283        USA: Morgan Kaufmann Publishers.
- 1284        Watanabe, Y., Wei, Q., Yang, D., Chen, X., Du, H., Yang, J., ... Miyazaki, N. (2008).  
1285        Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese  
1286        sturgeon. *Journal of Zoology*, 275, 381–390. doi:10.1111/j.1469-7998.2008.00451.x
- 1287        Watanabe, Y. Y., & Takahashi, A. (2013). Linking animal-borne video to accelerometers  
1288        reveals prey capture variability. *Proceedings of the National Academy of Sciences*, 110(6),  
1289        2199–2204. doi:10.1073/pnas.1216244110

- 1290 Weimerskirch, H. (2009). Editorial. In H. Ferro (Ed.), *30 years of wildlife tracking with*  
1291 *ARGOS* (p. 3). Cape Town, South Africa: CLS.
- 1292 Weimerskirch, H., Filippi, D. P., Collet, J., Waugh, S. M., & Patrick, S. C. (2018). Use of radar  
1293 detectors to track attendance of albatrosses at fishing vessels. *Conservation Biology*,  
1294 *32*(1), 240–245. doi:10.1111/cobi.12965
- 1295 Weimerskirch, H., Gault, A., & Cherel, Y. (2005). Prey distribution and patchiness: factors in  
1296 foraging success and efficiency of wandering albatrosses. *Ecology*, *86*(10), 2611–2622.  
1297 doi:10.1093/schbul/sbt124
- 1298 Weimerskirch, H., Pinaud, D., Pawlowski, F., & Bost, C. (2007). Does Prey Capture Induce  
1299 Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the  
1300 Wandering Albatross. *The American Naturalist*, *170*(5), 734–743. doi:10.1086/522059
- 1301 Weiser, A. W., Orchan, Y., Nathan, R., Charter, M., Weiss, A. J., & Toledo, S. (2016).  
1302 Characterizing the Accuracy of a Self-Synchronized Reverse-GPS Wildlife Localization  
1303 System. In *2016 15th ACM/IEEE International Conference on Information Processing in*  
1304 *Sensor Networks (IPSN)* (pp. 1–12). Vienna, Austria. doi:10.1109/IPSN.2016.7460662
- 1305 Wikelski, M., Kays, R. W., Kasdin, N. J., Thorup, K., Smith, J. A., & Swenson, G. W. (2007).  
1306 Going wild: what a global small-animal tracking system could do for experimental  
1307 biologists. *Journal of Experimental Biology*, *210*, 181–186. doi:10.1242/jeb.02629
- 1308 Williams, H. J., Holton, M. D., Shepard, E. L. C., Largey, N., Norman, B., Ryan, P. G., ...  
1309 Wilson, R. P. (2017). Identification of animal movement patterns using tri-axial  
1310 magnetometry. *Movement Ecology*, *5*, 6. doi:10.1186/s40462-017-0097-x
- 1311 Wilmers, C. C., Isbell, L. A., Suraci, J. P., & Williams, T. M. (2017). Energetics-informed  
1312 behavioral states reveal the drive to kill in African leopards. *Ecosphere*, *8*(6), e01850.  
1313 doi:10.1002/ecs2.1850
- 1314 Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015).  
1315 The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of  
1316 ecology. *Ecology*, *96*(7), 1741–1753.
- 1317 Wilson, K., Littman, C., Halpin, P., & Read, A. (2017). Integrating multiple technologies to  
1318 understand the foraging behaviour of Hawaiian monk seals. *Royal Society Open Science*,  
1319 *4*, 160703. doi:10.1098/rsos.160703
- 1320 Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F.,  
1321 ... Shepard, E. L. C. (accepted). Estimates for energy expenditure in free-living animals  
1322 using acceleration proxies; a reappraisal. *Journal of Animal Ecology*.
- 1323 Wilson, R. P., Cooper, J., & Plötz, J. (1992). Can we determine when marine endotherms feed?

- 1324 A case study with seabirds. *The Journal of Experimental Biology*, 167, 267–275.
- 1325 Wilson, R. P., Grant, W. S., & Duffy, D. C. (1986). Recording Devices on Free-Ranging  
1326 Marine Animals: Does Measurement Affect Foraging Performance? *Ecology*, 67(4),  
1327 1091–1093.
- 1328 Wilson, R. P., Grundy, E., Massy, R., Soltis, J., Tysse, B., Holton, M., ... Butt, T. (2014). Wild  
1329 state secrets: ultra-sensitive measurement of micro-movement can reveal internal  
1330 processes in animals. *Frontiers in Ecology and the Environment*, 12(10), 582–587.  
1331 doi:10.1890/140068
- 1332 Wilson, R. P., Holton, M. D., di Virgilio, A., Williams, H., Shepard, E. L. C., Lambertucci, S.,  
1333 ... Duarte, C. M. (2018). Give the machine a hand: A Boolean time-based decision-tree  
1334 template for rapidly finding animal behaviours in multisensor data. *Methods in Ecology  
1335 and Evolution*, 9, 2206–2215. doi:10.1111/2041-210X.13069
- 1336 Wilson, R. P., Holton, M. D., Walker, J. S., Shepard, E. L. C., Scantlebury, D. M., Wilson, V.  
1337 L., ... Jones, M. W. (2016). A spherical-plot solution to linking acceleration metrics with  
1338 animal performance, state, behaviour and lifestyle. *Movement Ecology*, 4, 22.  
1339 doi:10.1186/s40462-016-0088-3
- 1340 Wilson, R. P., Holton, M., Wilson, V. L., Gunner, R., Tysse, B., Wilson, G. I., ... Scantlebury,  
1341 D. M. (2019). Towards informed metrics for examining the role of human-induced animal  
1342 responses in tag studies on wild animals. *Integrative Zoology*, 14, 17–29.  
1343 doi:10.1111/1749-4877.12328
- 1344 Wilson, R. P., & Liebsch, N. (2003). Up-beat motion in swinging limbs: New insights into  
1345 assessing movement in free-living aquatic vertebrates. *Marine Biology*, 142(3), 537–547.  
1346 doi:10.1007/s00227-002-0964-9
- 1347 Wilson, R. P., Neate, A., Holton, M. D., Shepard, E. L. C., Scantlebury, D. M., Lambertucci,  
1348 S. A., ... Marks, N. (2018). Luck in Food Finding Affects Individual Performance and  
1349 Population Trajectories. *Current Biology*, 28(23), 3871–3877.e5.  
1350 doi:10.1016/j.cub.2018.10.034
- 1351 Wilson, R. P., Scolaro, A., Quintana, F., Siebert, U., thor Straten, M., Mills, K., ... Müller, G.  
1352 (2004). To the bottom of the heart: cloacal movement as an index of cardiac frequency,  
1353 respiration and digestive evacuation in penguins. *Marine Biology*, 144, 813–827.  
1354 doi:10.1007/s00227-003-1247-9
- 1355 Wilson, R. P., Simeone, A., Luna-Jorquera, G., Steinfurth, A., Jackson, S., & Fahlman, A.  
1356 (2003). Patterns of respiration in diving penguins: is the last gasp an inspired tactic? *The  
1357 Journal of Experimental Biology*, 206, 1751–1763. doi:10.1242/jeb.00341

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- 1358 Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A., & Murita, M. (2002). Lip-reading  
1359 in remote subjects: an attempt to quantify and separate ingestion, breathing and  
1360 vocalisation in free-living animals using penguins as a model. *Marine Biology*, *140*, 17–  
1361 27. doi:10.1007/s002270100659
- 1362 Xavier, G., & Dodge, S. (2014). An exploratory visualization tool for mapping the relationships  
1363 between animal movement and the environment. *Proceedings of the 2nd ACM*  
1364 *SIGSPATIAL International Workshop on Interacting with Maps - MapInteract '14*, 36–  
1365 42. doi:10.1145/2677068.2677071
- 1366 Yang, G.-Z. (2014). *Body Sensor Networks*. London, UK: Springer-Verlag.
- 1367 Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., ... Le Maho,  
1368 Y. (2001). A new technique for monitoring the behaviour of free-ranging Adélie penguins.  
1369 *The Journal of Experimental Biology*, *204*, 685–690. doi:10.1016/s0304-3959(97)00161-  
1370 9
- 1371 Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C.-A., Le Maho, Y., & Naito, Y. (1999).  
1372 Precise monitoring of porpoising behaviour of Adélie penguins determined using  
1373 acceleration data loggers. *The Journal of Experimental Biology*, *202*, 3121–3126.
- 1374