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1 **Give the machine a hand: A Boolean time-based decision-tree template for**
2 **rapidly finding animal behaviours in multi-sensor data**

3
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24
25
26
27 **Abstract**

- 28
29 **1.** The development of multi-sensor animal-attached tags, recording data at high
30 frequencies, has enormous potential in allowing us to define animal behaviour.
31 **2.** The high volumes of data, are pushing us towards machine-learning as a powerful option
32 for distilling out behaviours. However, with increasing parallel lines of data, systems

33 become more likely to become processor limited and thereby take appreciable amounts
34 of time to resolve behaviours.

- 35 3. We suggest a Boolean approach whereby critical changes in recorded parameters are
36 used as sequential templates with defined flexibility (in both time and degree) to
37 determine individual behavioural elements within a behavioural sequence that, together,
38 makes up a single, defined behaviour.
- 39 4. We tested this approach, and compared it to a suite of other behavioural identification
40 methods, on a number of behaviours from tag-equipped animals; sheep grazing, penguins
41 walking, cheetah stalking prey and condors thermalling.
- 42 5. Overall behaviour recognition using our new approach was better than most other
43 methods due to; (i) its ability to deal with behavioural variation and (ii) the speed with
44 which the task was completed because extraneous data are avoided in the process.
- 45 6. We suggest that this approach is a promising way forward in an increasingly data-rich
46 environment and that workers sharing algorithms can provide a powerful library for the
47 benefit of all involved in such work.

48 49 **1 | INTRODUCTION**

50
51 Animal behaviour has been variously defined, but generally can be defined as ‘the way in which
52 an animal works, functions or responds to a particular situation’ (Tinbergen 1960) with
53 consequences for lifetime reproductive success (Birkhead, Atkin & Møller 1987; Drews 1993;
54 Krebs, Davies & Parr 1993; Krebs & Davies 2009). As such, our ability to determine animal
55 behaviours precisely is critically important for proper understanding of animal ecology and
56 ecosystem functioning (Krebs, Davies & Parr 1993). Indeed, it is this that explains the large
57 variety of methodologies developed to quantify behaviour (e.g. Tinbergen 1960; Altmann 1974;
58 Lucas & Baras 2000; Miller & Gerlai 2007; Chastin & Granat 2010). A particularly rapidly
59 developing field in this regard is ‘biologging’ – the deployment of autonomous tags on animals
60 to record data (Hooker *et al.* 2007). Specifically, the extraordinary development of electronic
61 technology over the last 3 decades has led the progression of sophisticated miniature sensors
62 coupled with low power consumption and rapidly expanding memory capacity (Ropert-Coudert
63 & Wilson 2005) so that studies using multi-sensor technology in tags on animals are now
64 common (Brown *et al.* 2013). This has led from the simple animal-attached tags of the 1990s
65 recording data once every few seconds (Wilson *et al.* 1994), to systems today that may record

66 multiple channels at thousands of Hertz (Johnson & Tyack 2003). Of particular note for defining
67 behaviours is the role played by accelerometers, gyroscopes and magnetometers, which can
68 resolve both animal attitude in the 3 spatial axes (Yoda *et al.* 1999; Williams *et al.* 2017) and
69 movement (Fourati *et al.* 2011; Noda *et al.* 2014). These are primary elements used in classifying
70 behaviours (Tinbergen 1960), and so have great potential in studies of wild animals.

71 However, the ease with which we can now record the physical manifestation of
72 behaviour, *via* metrics such as pitch, roll and ‘dynamism’ in the acceleration signature (Laich *et*
73 *al.* 2008), is tempered by the difficulties of dealing with the complexity and volume of such data.
74 Thus, computational solutions for processing the signals are inevitable and, accordingly, there is
75 a rich and varied literature dealing with this (e.g. Sakamoto *et al.* 2009; Nathan *et al.* 2012;
76 Resheff *et al.* 2014). This includes support vector machines (Tachibana, Oosugi & Okanoya
77 2014), regression trees (de Weerd *et al.* 2015), random forests (Bidder *et al.* 2014), neural
78 networks (Samarasinghe 2016), linear discriminant analysis (Anderberg 2014) and template-
79 matching (Walker *et al.* 2015b). Each method has advantages and disadvantages (Resheff *et al.*
80 2014) but prime negative issues revolve around subjectivity, whether the data are parametric, the
81 extent of over-fitting, and the computational time involved in the process (Nathan *et al.* 2012).
82 In addition, a particular weakness of many systems is that they fail to recognise the temporal
83 sequencing of the movements that define the fundamental unit of that behaviour and the
84 variability within them, and thereby preclude an important discriminator. For example, walking
85 may be defined by a cluster of acceleration metrics (Bidder *et al.* 2014) but the fundamental unit
86 of walking is the single step (Moe-Nilssen & Helbostad 2004) and this has well-defined
87 properties over time (Sabatini *et al.* 2005) that could, for example, be used in any decision tree-
88 based approach.

89 In this paper, we present an approach for identifying behaviours from data derived from
90 animal-attached tags that recognises (i) the lowest common denominator (LoCoD) defining any
91 particular behaviour (i.e. a single step is the lowest common denominator within walking) and
92 (ii) that this lowest common denominator can be usefully broken down into base elements (BEs)
93 (such as an increase, followed by a drop, in dorso-ventral acceleration for walking (Rong *et al.*
94 2007)), all of which have to follow each other in a defined sequence for the LoCoD to be
95 apparent. Finally, (iii), the timing of BEs within a sequence is often constrained. Thus, this
96 process provides a recognizable key for LoCoDs of behaviours based on measurements,
97 sequences and timings of BEs. We appreciate that much of the essence of this is inherent in some
98 template-matching approaches (Walker *et al.* 2015a) but combine this with both temporal

99 flexibility across all BEs, together with an ability to switch between and incorporate defined,
100 often derived, metrics that provide critical information for a powerful match. We demonstrate
101 the utility of this approach by using it to search for behaviours that have LoCoD periods ranging
102 between fractions of a second and several minutes using data derived from animal-attached tags
103 and compare it briefly to other computational methods.

104

105 **2 | MATERIALS AND METHODS**

106

107 For this approach, we consider primary data derived from orthogonal, tri-axial accelerometers
108 as well as, where helpful, information from pressure- and magnetic sensors, in addition to
109 calculated variables obtained from acceleration data, such as Vectorial Dynamic Body
110 Acceleration (VeDBA) (Qasem *et al.* 2012).

111

112 **2.1 | The LoCoD Method**

113

114 The LoCoD method involves initial consideration of the data visually by the user, who should
115 examine the details of the movement that makes up the behaviour and reflect how this movement
116 is expected to affect the sensors. In this, the user should identify the patterns that make up the
117 BEs of the LoCoD and whether they can be made more distinctive by selective smoothing, as is
118 done in many behaviour-identifying protocols anyway (Nathan *et al.* 2012). In addition, it is
119 recommended that differentials be derived for any signals of interest, since these often act as
120 excellent thresholds in derivation of the BEs (Fig. 1). Differentials are particularly important
121 since postural data derived from acceleration (Shepard *et al.* 2008) are dependent, in part, on the
122 angle of the terrain beneath the study animal (cf. the difference in sway axis during the stationary
123 periods at the beginning and end of the walking period in Fig. 1), as well as the tag placement.
124 Thus, working with differentials essentially standardises the signal output.

125

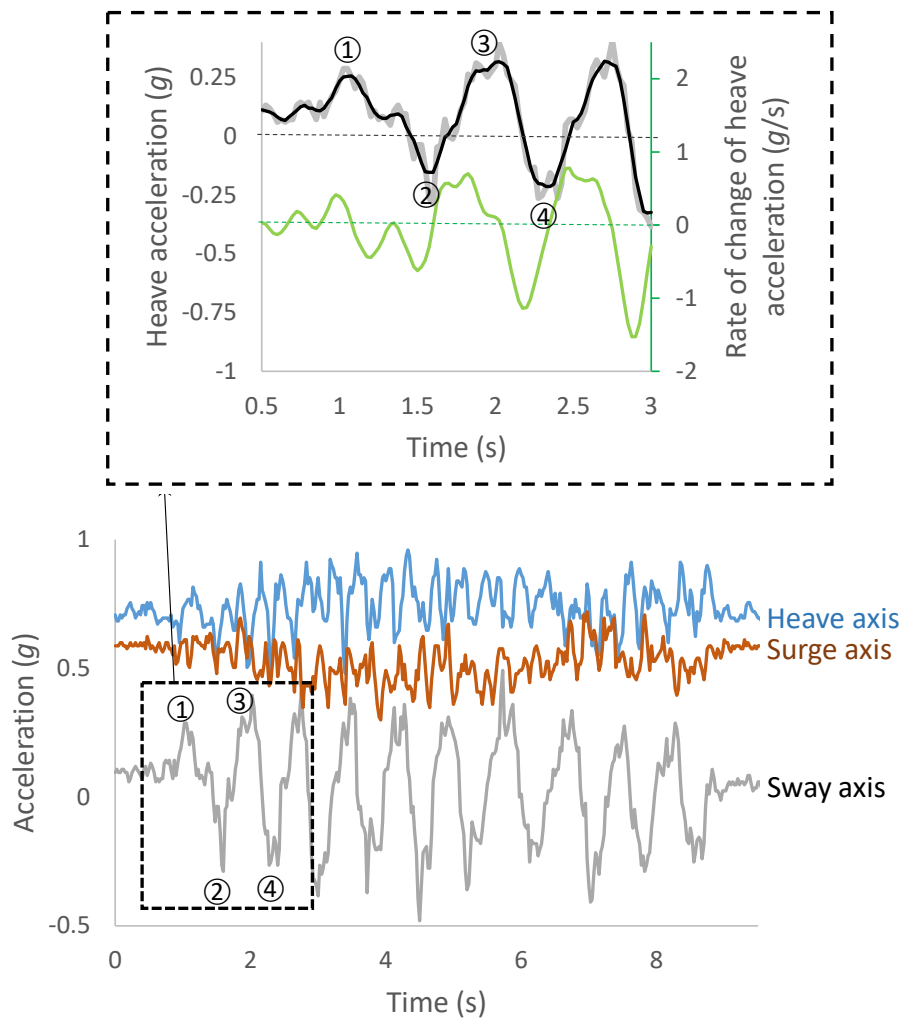


Fig. 1 – Twenty steps (the first 4 numbered) taken by a Magellanic penguin *Spheniscus magellanicus* during walking on the beach, manifest by tri-axial acceleration data at 40 Hz. The bird starts and ends stationary, but begins to walk, with 2 small steps before rapidly changing to steps with clear waveforms, particularly in the sway (lateral) axis (grey line). Within the LoCoD framework, the user is expected to identify the most useful primary data streams for the process. These may be expanded by deriving secondary data streams, such as smoothed values, to enhance BE identification. The inset shows the first 5 steps (grey line) smoothed over 0.125 s (black line) in the dominant waveform (the sway axis) and the rate of change of the smoothed data (green line).

126
 127 Following decisions on which channels are to be used for identification of the behaviour,
 128 the conditions describing each BE are set up in ordered sequence to describe the LoCoD. Each
 129 summary condition for the BE follows a Boolean approach. For example, summary condition 1
 130 that defines BE₁ of the LoCoD for a penguin walking (Fig. 2) may be asked to recognise the
 131 moment when the differential of the smoothed sway acceleration exceeds 0.25 g/s;

132

133 BE₁ - RECOGNISE WHEN; $dA_h/dt > 0.25 \text{ g/s}$ (1)

134

135 where Ah_s is the smoothed heave acceleration following;

136
137
$$Ahs = \frac{1}{n} \sum_{i=0}^{n-1} Ah - i \tag{2}$$

138

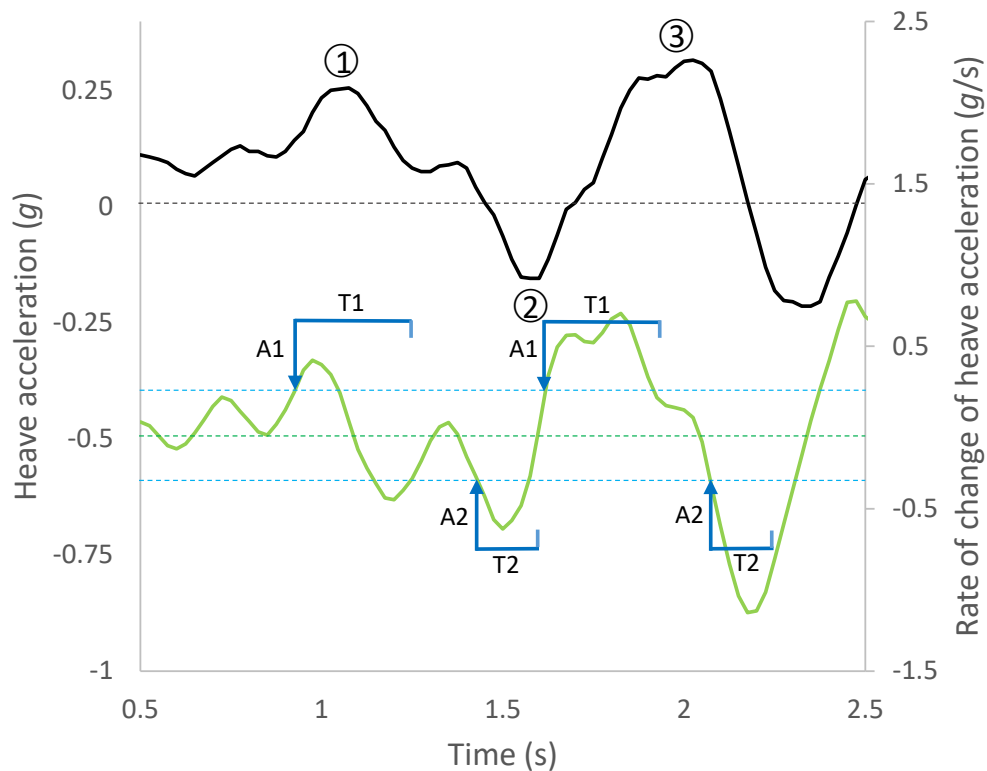


Fig. 2 – The first 3 steps (numbered) of the walking period shown in Fig. 1 for the smoothed heave axis (black line) and the rate of change of the heave axis (green line). The LoCoD method first identifies a feature, or combination of features, that signify the initiation of the first BE of the behaviour (here a differential threshold of $>0.25 \text{ g/s}$) (marked A1). There is then a defined ‘dead’ time (T1), over which the program skips before looking for the second BE defining the behaviour (here a differential threshold of $<-0.25 \text{ g/s}$) (A2) with its ‘dead’ time (T2). If these two conditions are met (as in this case) the LoCoD is made of 2 BEs and describes the conditions for one left stride followed by one right stride. The process could, however, be used for strides from one leg only, for example, whereupon either just A1 and T1 or A2 and T2 would be used for left and right strides, respectively.

139

140

141 In addition, the process should recognise multiple, cross-channel sub-conditions (for positives
142 and negatives). Thus, equation (1) might be made of 3 sub-conditions;

143

144 BE₁ - RECOGNISE WHEN; $dAh_s/dt > 0.25 \text{ g/s}$

145 AND; $dA_s/dt > 0.05 \text{ g/s}$
 146 AND NOT; $D > 0 \text{ m}$ (3)

147

148 where A_s is the surge acceleration and D is the depth.

149

150 Importantly, each sub-condition or condition can employ a time base with three elements within
 151 it that can be specified. These are;

152

- 153 1. *Presence* - that the sub-condition or condition is maintained over a specified time for the
 154 statement to be TRUE
- 155 2. *Range* - that, following identification of a true sub-condition or condition, the program
 156 can skip a defined number of data points before looking for the next BE. This is important
 157 because it can stop the program identifying multiple adjacent points as multiples of that
 158 BE, moving directly onto a search for the next BE.
- 159 3. *Flexibility* - that the length of time over which the next BE may occur can be defined
 160 within limits.

161

162 Thus, in the example above, recognition of BE₁ followed by BE₂ to give a LoCoD for one left
 163 stride followed by one right stride (Fig. 2) could be;

164

165 (BE₁) *Presence* WHEN; $dA_{h_s}/dt > 0.25 \text{ g/s}$ FOR $t > 0.2 \text{ s}$ IS TRUE
 166 (BE₁) *Range* SKIP DATA FOR 0.25 s
 167 (BE₂) *Flexibility* WHEN; $dA_{h_s}/dt < -0.25 \text{ g/s}$ FOR $t > 0.2 \text{ s}$ WITHIN $t = 0.3 \text{ s}$ OF END OF
 168 BE₁

169

170 The value of the time-based definition is that it helps deal with variation in both amplitudes and
 171 periods of waveforms. Specifically, it allows the program to;

- 172 (a) be less susceptible to outliers (cf. *Presence*),
- 173 (b) detect the beginning of e.g. a waveform (cf. A1 in Fig. 2) and then allows flexibility in
 174 time to pass the peak of that waveform (cf. *Range*)
- 175 (c) constrain the length of time within which the next sub-element must occur for it to be
 176 considered part of the LoCoD (cf. *Flexibility*).

177 We present the computational process by which the data are treated using the LoCoD method
178 in the supplementary material 1 but also note the following link
179 (<http://ggluck.swan.ac.uk/ftp/DDMT%20new%20version/>) where the software can be downloaded.

180

181 *Suggestions for defining Behavioural Elements*

182 Although behavioural elements can be defined by simple inspection, the variability in the way
183 they are manifest and the limits set to define them by the user are critical to the success of the
184 overall algorithm for identifying behaviours. We suggest that the user first inspects the data in
185 the form of line graphs over time to identify which data streams change predictably with the
186 behaviour to be isolated. At this stage, the data can also be smoothed to reduce noise. In general,
187 we note that running means are particularly valuable for smoothing out short-term outliers,
188 diminishing noise and highlighting the major trends in waveforms; within the program above,
189 the user can experiment with different smoothing windows to produce the clearest waveform in
190 the data (cf. Fig. 1). Each data line to be used in the identification of a BE can then be cut from
191 a number of examples of the BE in the data (ideally from a number of different animals) and
192 these examples effectively superimposed on each other to show the variability in the data (Fig.
193 3). The same data can then be used to work out mean (and variance) numeric values for the
194 parameters to be used in the (sensor value-based or time-based) rules to define a BE (Fig. 3).
195 Consideration of the spread of the distribution of values of such parameters allows users to assess
196 the extent to which the chosen thresholds will work within a population of the BEs.

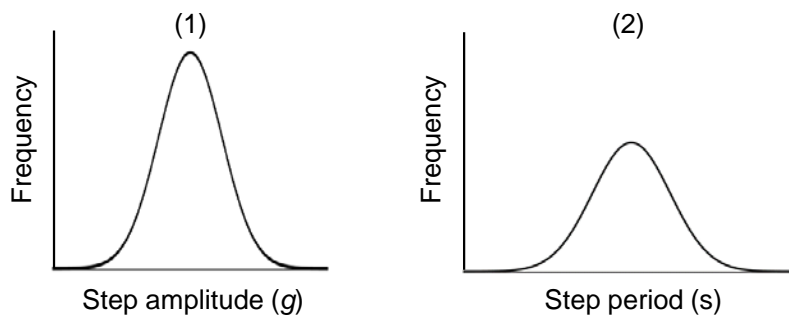
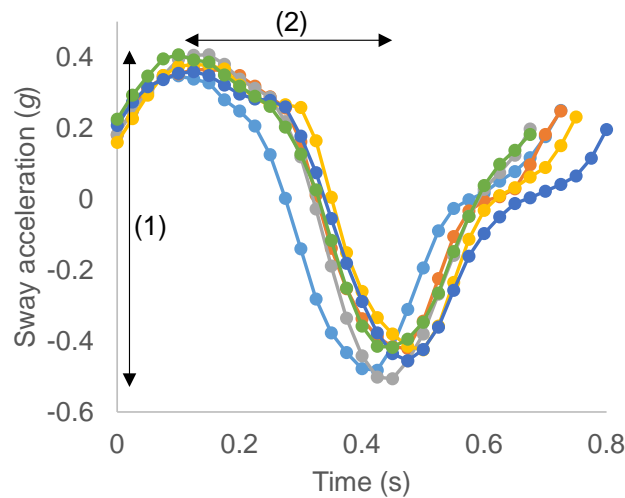


Fig. 3 – Example of the process of defining the value of parameters used to identify behavioural elements in the LoCoD method. The upper graph shows multiple examples of a given behaviour (penguin walking) in a recorded data stream that represents the behaviour well (in this case the smoothed sway acceleration). The superimposition of multiple examples of the behaviour highlights the variation in the behaviour. Construction of frequency distributions of particular elements that could be used to define a behavioural element (here step amplitude (1) and step period (2)) provide information on the probabilities of any given step falling outside user-defined limits to that distribution. This ultimately defines the extent to which the criteria will encompass the defined behavioural element.

197
 198 In order to test the applicability of the LoCoD method over different behavioural periods, we
 199 used animal data corresponding to;
 200
 201 (a) 'Short-period' LoCoDs of behaviours, manifested by actions typically lasting less than 1
 202 s: The examples used for this study were single bites of sheep and single steps by
 203 penguins walking.

204 (b) 'Medium-period' LoCoD of behaviours, typically lasting several seconds: The example
205 used here was condors thermalling.

206 (c) 'Long-period' LoCoD of behaviours, typically lasting from between 30 s up to minutes:
207 Here, we used cheetahs stalking prey.

208
209 A training dataset was created for behavioural identification for each of the above species, where
210 all cases of the given behaviour was identified either according to known instances where the
211 behaviour had been directly observed, or recorded, or by manual identification by an expert (see
212 Supplementary material for behaviour descriptions and LoCoD definitions).

213 The LoCoD method was compared to other methods, see below, by considering the
214 following metrics to assess classification performance: (1) Processing time (in seconds), which
215 is the time spent by our single computer (to ensure that processing capacity was the same for all
216 tasks) to identify and classify behaviours within defined data sets, and (2) Confusion Matrix-
217 based scores: These metrics include Recall and Precision, which are routinely used in such
218 comparisons (Resheff *et al.* 2014). Recall (also known as Sensitivity or True Positive rate) is
219 estimated as: $\text{True Positives} / (\text{True Positives} + \text{False Negatives})$; and Precision is estimated as:
220 $\text{True Positives} / (\text{True Positives} + \text{False Negatives})$. These two metrics are interesting because
221 when Recall values increase, Precision values decrease, and we can assess the performance of a
222 model by focusing the balance between both measures. By calculating both, we have a measure
223 that expresses the ability of the model to find a particular behaviour in the dataset (i.e., Recall)
224 while we have also a measure that expresses the proportion of the data points that our model
225 classified as a particular behaviour that actually was that behaviour (i.e., Precision). We do not
226 present Accuracy values for two reasons; i) since the LoCoD method does not consider each data
227 point individually, quantification of the identification result of a given LoCoD case cannot give
228 a true negative result and; ii) although true negative results can be established with the machine-
229 learning methods, Accuracy can give biased results for unbalanced data sets (i.e., when the
230 number of true positives in the confusion matrix is very different to the true negative (Sokolova
231 & Lapalme 2009; Stapor 2017).

232

233 **2.2 | Comparator methods**

234

235 We compared the outputs of the LoCoD method with nine different behavioural classifier
236 models. These were; (1) K-Nearest Neighbours (K=3), (2) Linear Support Vector machines

237 (Linear SVM), (3) Radial Basis Function kernels for Support Vector Machines (RBF SVM), (4)
238 Decision Trees, (5) Random Forest, (6) Naïve Bayes, (7) Linear Discriminant Analysis (LDA),
239 (8) Quadratic Discriminant Analysis (QDA), (9) Artificial Neural Networks (ANN). These are
240 all offered within a single piece of software as freeware (AccelerRater, [http://accapp.move-ecol-
242 minerva.huji.ac.il/](http://accapp.move-ecol-
241 minerva.huji.ac.il/)) (Resheff *et al.* 2014) which facilitates protocols and testing (see a brief
243 description of each model in Supplementary material). When using AccelerRater, we used the
244 ‘all features’ option to construct the models (selecting the “*precomputed stats, Label*” option from
245 the upload tab, to ensure that we could have available the same features employed with LoCoD)
246 and a Train-Test split (50% for training and 50% for testing) for validation as for the LoCoD
247 method. We note though, that machine learning methods have numerous options for fine tuning,
248 which can have an appreciable impact on the overall accuracy (Ladds *et al.* 2017) so our
249 comparison between machine learning options and the LoCoD method may have disadvantaged
250 the machine learning process.

250

251 3 | RESULTS

252

253 The overall capacity of the LoCoD method to detect specified behaviours within varied datasets
254 from free-living animals, was comparable, and sometimes higher, to some of the best methods
255 otherwise tested (Tables 1 and 2). However, the speed with which the LoCoD method resolved
256 behaviours was many times faster than the more conventional methods. For instance, the time
257 required for the LoCoD method to process sheep biting and condor thermalling was less than
258 1% of the time required for the best machine-learning algorithm (representing 0.04% and 0.41%,
259 respectively). In the case of the cheetah and the penguin data, the time required for the LoCoD
260 method to classify the walking represented 6% and 20% of the total time required for the best
261 machine-learning algorithm (Tables 1 & 2).

262 For sheep biting, although the best machine-learning algorithm (considering shortest
263 processing time, together with highest recall and precision) was the QDA method, none of the
264 used machine-learning algorithms had a good overall performance for classification (Table 1).
265 The LoCoD method was the only approach that showed good performance in all the Confusion
266 Matrix based scores (all above 85%).

267 For penguin walking, there were 4 machine-learning algorithms that showed similar
268 performance for all metrics (Nearest Neighbour, RBF SVM, Decision Tree, and Random Forest).

269 The LoCoD method showed similar performance (Recall and Precision above 95%) but with
270 processing times that were a fraction of the best machine-learning approaches (Table 1).

271 Although the best machine-learning method to classify condor thermalling was QDA,
272 most of the methods resulted in poor performance, with most requiring excessive processing
273 times and some even unable to provide a result (marked as NA in Table 2). The LoCoD method
274 showed comparable performance to QDA, with lower Recall, higher Precision and notably lower
275 processing times, equating to about 0.4% that of the QDA (Table 2). Although markedly slower
276 than the LoCoD method (it took almost 250 times longer), the manual method outperformed all
277 other options by an extended margin (Table 2).

278 In a manner similar to condor thermalling, most of the methods attempting to define
279 cheetah stalking resulted in poor performance, many of them requiring excessive processing
280 time, with the software from some systems unable to provide a result (marked as NA in Table
281 2). The best machine-learning method was Decision Tree. The LoCoD method showed
282 comparable performance to this, with an approximately 10% lower Recall and Precision, but
283 with significantly lower processing times, equating to about 6% that of the Decision Tree method
284 (Table 2).

285 Overall, and of particular note, was that the LoCoD method dealt particularly well with
286 behavioural identification where the temporal variability of the behaviour was high (defined by
287 the range in duration of the different base elements of the behaviour). For example, in the case
288 of the condor thermalling, manual labelling showed that each complete turn had a mean duration
289 of 19.7 ± 4.9 s (SD), showing the variation in the presence, range and flexibility (cf. Fig. 3) of
290 the two base elements used to define this behaviour (based on altitude gain and rates of change
291 of magnetometry data - Supplementary Data, Table S3.3). Given that the sum of these three
292 values limits the maximum duration of the LoCoD, all but one of the labelled LoCoD complete
293 turns in thermal soaring were 15 seconds in duration. Similarly, where the machine-learning
294 methods struggled with identification of the cheetah stalking, the LoCoD method performed
295 well; the temporal range of this behaviour being 48.3 ± 16.2 s.

296
297 **TABLE 1** Performance and time taken for the different identification methods to identify all
298 cases of the ‘short-period’ behaviour of sheep biting and penguin walking in their respective data
299 sets (see supplementary material for further detail). For each method, the time taken for the
300 algorithm to run through the complete data set is given, along with the measures of recall and
301 precision.

<i>Method</i>	<i>Sheep biting</i>			<i>Penguin walking</i>		
	Time (s)	Performance		Time (s)	Performance	
		Recall	Precision		Recall	Precision
<i>Manual</i>	2039	1.00	1.00	2040	1.00	1.00
<i>LoCoD</i>	1.5	0.89	0.87	14	0.98	0.98
<i>Nearest Neighbour</i>	243	0.00	0.00	77	0.97	0.96
<i>Linear SVM</i>	3189	0.00	0.00	359	1.00	0.75
<i>RBF SVM</i>	253	0.00	0.00	79	0.94	0.97
<i>Decision Tree</i>	242	0.00	0.00	80	0.97	0.96
<i>Random Forest</i>	281	0.00	0.00	82	0.98	0.96
<i>Naïve Bayes</i>	317	0.00	0.00	75	0.99	0.76
<i>LDA</i>	264	0.00	0.00	74	0.99	0.76
<i>QDA</i>	353	0.99	0.01	77	0.76	0.71
<i>ANN</i>	3451	0.00	0.00	405	0.92	0.97

305 **TABLE 2** Performance and time taken for the different identification methods to identify all
306 cases of ‘medium-period’ behaviour, consisting of condor thermalling and the ‘long-period’
307 behaviour of cheetah stalking in their respective data sets (see supplementary material for further
308 detail). For these two behaviours, a number of machine-learning methods were not run to
309 completion due to some system error, generally after more of 20 hours of processing time
310 (marked with NA). For each method, the time taken for the algorithm to run through the complete
311 data set is given, along with the measures of recall, and precision.

312

<i>Method</i>	<i>Condor thermalling</i>			<i>Cheetah stalking</i>		
	Time (s)	Performance		Time (s)	Performance	
		Recall	Precision		Recall	Precision
<i>Manual</i>	2220	1.00	1.00	180	1.00	1.00
<i>LoCoD</i>	9	0.87	0.73	7.2	0.89	0.89
<i>Nearest Neighbour</i>	2182	0.14	0.26	4045	0.99	0.98
<i>Linear SVM</i>	NA	NA	NA	NA	NA	NA
<i>RBF SVM</i>	NA	NA	NA	NA	NA	NA
<i>Decision Tree</i>	2358	0.01	0.35	3470	0.99	0.99
<i>Random Forest</i>	2998	0.00	0.00	4217	1.00	0.98
<i>Naïve Bayes</i>	NA	NA	NA	3179	0.19	0.03
<i>LDA</i>	2152	0.01	0.01	3016	0.06	0.26
<i>QDA</i>	2157	0.54	0.91	NA	NA	NA
<i>ANN</i>	NA	NA	NA	NA	NA	NA

313

314

315 4 | DISCUSSION

316

317 4.1 | Speed versus accessibility considerations in identifying behaviours

318

319 In his seminal work on behaviour, Tinbergen (Tinbergen 1960) defined behaviours by noting
320 prescribed changes in animal movement over time. This approach gets to the heart of behaviour

321 description and is one that should be accessible by those using animal-attached sensors, e.g.
322 accelerometers, magnetometers and gyroscopes (Johnson & Tyack 2003), that record body
323 postures and movement in its various forms over time. Indeed, the precision with which
324 movement descriptors such as angular velocity and acceleration can be measured has catalysed
325 many studies of animal behaviour by workers using such smart tags (Yoda *et al.* 1999). More
326 information about the movement from multiple sensors, many of which measure tri-axially to
327 cover the 3 space dimensions anyway (Johnson & Tyack 2003; Wilson, Shepard & Liebsch
328 2008), can lead to very comprehensive descriptions of movement (Yoda, Kohno & Naito 2004),
329 something that can be further enhanced by converting primary movement data (such as
330 acceleration) to additional derivatives (such as VeDBA (Qasem *et al.* 2012)). Interpretation of
331 such diverse and complex data is not intuitive, which makes a good case for machine-learning
332 since no specialised knowledge is required by users. Coupled with this is the expectation that
333 machine-learning systems produce best classifications if they are provided with most data, which
334 makes a clear case for using all possible data (Resheff *et al.* 2014). However, this brings with it
335 appreciable computational challenges because every new line of information has to be
336 considered computationally with respect to all others. Processing time therefore increases
337 disproportionately with the inclusion of every new data stream (Murphy 2012). Indeed, although
338 computer processing speed continues to increase roughly according to Moore's Law, so too does
339 our capacity to log data (Schaller 1997). Our ability to incorporate new sensors within our
340 animal-attached tag systems (Robert-Coudert & Wilson 2005), coupled with a proclivity to
341 record at ever faster rates (Robert-Coudert & Wilson 2004) and derive new metrics from the
342 base data (e.g. jerk, static- and dynamic acceleration as well as dynamic body acceleration from
343 raw tri-axial acceleration data (Ydesen *et al.* 2014)) in tandem with tag deployments that may
344 span months bringing in billions of prime data points, inevitably leads to more extended
345 computing times.

346 Such a compromise might be more acceptable if the performance of machine-learning
347 approaches was exceptional, but our results show that this is not the case (Tables 1 & 2). Our
348 LoCoD approach requires good understanding and careful inspection of the sensor channels in
349 order to make decisions about which data streams are most useful (and in which combination)
350 to define the behaviour. This therefore requires some degree of specialist knowledge of the
351 sensors used and an appreciable initial investment in time, although we would advocate that any
352 use of sensor-acquired data 'blind' is not good practice anyway. Our suggestion is that the
353 LoCoD approach specifically follows a 3 stage process; (1) where the primary data streams of

354 interest are signal-processed to reduce noise and highlight patterns (e.g. via smoothing) over
355 various scales, (2) where derived data streams, most notably differentials, are calculated for
356 inclusion, if relevant (based on expectations and inspection of the behaviour in question) and (3)
357 where conditions for sequential BEs are defined based on precise patterns in selected data
358 streams with defined time-dependent flexibility for their execution. Such an approach is
359 obviously more onerous for the worker than a machine-based learning technique and may be
360 considered a disadvantage. However, this approach frees up appreciable amounts of
361 computational time (Tables 1 & 2) by directing the machine to deal rapidly with a small fraction
362 of the available data. This is critical for complex behaviours made up of many BEs. In the
363 process, it allows identification of the minutia of behaviour if needed (e.g. left footsteps rather
364 than ‘walking’) which may be important for rare, very short-lived behaviours. Indeed, the
365 LoCoD method specifically identifies the smallest common denominator that defines a
366 behaviour according to the sequence of BEs, for example single steps, or pairs of steps, within
367 walking, rather than general walking *per se*. This leads to apparent overkill in that the approach
368 will essentially identify every step during the tagged period, which may be more detail than many
369 need, but steps within a defined time interval of each other can be merged without problem to
370 produce larger bouts of walking if preferred and analysed according to behavioural type.
371 Conversely, identification of slow, single steps, such as occur when herbivores graze, can lead
372 to appreciable displacement over time, so their identification can be important in dead-reckoning
373 approaches for resolving animal movement (Bidder *et al.* 2015). In addition, the ability to
374 separate, for example, ‘grazing and walking’ from ‘grazing without walking’ should allow
375 workers to recognise sub-behaviours within behaviours, something that is considered by people
376 observing animals (Beker *et al.* 2010) but which are normally overlooked in tag data
377 (Martiskainen *et al.* 2009). The LoCoD method performed slightly less well with our example
378 of long-period behaviours than with short- or medium-period behaviours (Tables 1 & 2) making
379 it apparently less useful (although the behaviour was identified in <0.5% of the time taken for
380 the manual or machine-learning approach). Ultimately though, the absolute value of the approach
381 depends on the extent to which the variability of the behaviour can be described by the flexibility
382 of the algorithm used (see above). More work will be needed to determine the extent to which
383 our results for cheetahs stalking are typical of ‘long-lived’ behaviours.

384

385 **4.2 | Libraries of behaviours and inter-specific interpolation**

386

387 An obvious advantage of explicitly defining an algorithm for a particular behaviour is that it can
388 be stored and used for different individuals (cf. Fig. 3). However, a particular strength of the
389 process of defining LoCoDs via BEs extends beyond this. This is because algorithms can be
390 compared inter-specifically, and cognisance taken of changing values within the individual BEs
391 to help predict what might be expected for new species. For example, the details of locomotion
392 are known to be a broad function of mammal size and leg length (Christiansen 2002) so BEs
393 coding for this should change in their specified conditions accordingly. Indeed, such specified
394 conditions could be regressed against e.g. body mass to make predictions. As part of this general
395 process, we anticipate that an online library could be created, which provides effective
396 algorithms for determination of defined behaviours, which workers may readily consult for their
397 own applications. Success in this venture may result in researchers using such algorithms without
398 particular comprehension or time invested so that user expertise might eventually mirror those
399 that employ machine-learning techniques. Against this, inter-specific variation beyond simple
400 allometric expectations may serve to reduce the performance of this proposed cross-species
401 approach (see Campbell *et al.* 2013). Either way though, having access to a defined method of
402 determining the BEs within LoCoDs for behaviours for one species should certainly serve as a
403 very useful starting point for users wishing to examine the same behaviour in another.

404

405 **5 | Conclusions**

406

407 Although the LoCoD method described here requires appreciable investment in time and
408 understanding for workers to be able to develop appropriate algorithms for BEs, the approach
409 clearly has value for those wishing to extract behaviours from multi-sensor data. The approach
410 does not require a fixed sliding time window to operate, but has built-in flexibility in both time
411 and amplitude to recognise patterns and, in addition, can be made to be 'blind' for a period within
412 BEs so as not to be confused by the vagaries of variability at certain points within waveforms.
413 This flexible template tactic, which uses a Boolean approach on only the bare minimum of data
414 needed to recognise behaviours (ranging from those lasting less than 1 second to minutes or even
415 hours, (cf. Horie *et al.* 2017), frees up processing time, making the whole process substantially
416 more efficient. We would hope that algorithms for defined behaviours from particular species
417 will be shared within the community to build up a potent library for the benefit of all wishing to
418 try the approach.

419

420

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437

438 **AUTHORS' CONTRIBUTIONS**

439

440 RPW and MH conceived and developed the methodology, with input from all other authors.
441 AdV, ELCS, FQ, JES, DMS and SL collected the data. AdV and HW tested various data sets
442 with the algorithms and various machine-learning software and all authors contributed critically
443 to the development of, and writing, the manuscript.

444

445 **DATA ACCESSIBILITY**

446

447 The data used in this work are deposited within Dryad.

448

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