





Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data

Rory P. Wilson¹  | Mark D. Holton² | Agustina di Virgilio^{3,4} | Hannah Williams¹  | Emily L. C. Shepard¹ | Sergio Lambertucci³  | Flavio Quintana⁵ | Juan E. Sala⁵ | Bharathan Balaji⁶ | Eun Sun Lee⁶ | Mani Srivastava⁶ | D. Michael Scantlebury⁷  | Carlos M. Duarte⁸

¹Department of Biosciences, College of Science, Swansea University, Swansea, UK; ²Department of Computing Science, College of Science, Swansea University, Swansea, UK; ³Grupo de Biología de la Conservación, Laboratorio Ecotono, INIBIOMA (CONICET-Universidad Nacional del Comahue), Bariloche, Argentina; ⁴Grupo de Ecología Cuantitativa, INIBIOMA (CONICET-Universidad Nacional del Comahue), Bariloche, Argentina; ⁵Instituto de Biología de Organismos Marinos IBIOMAR-CONICET (9120), Puerto Madryn, Chubut, Argentina; ⁶Department of Electrical and Computer Engineering, University of California, Los Angeles, Los Angeles, California; ⁷School of Biological Sciences, Institute for Global Food Security, Queen's University Belfast, Belfast, UK and ⁸Red Sea Research Centre, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia

Correspondence

Rory P. Wilson

Email: r.p.wilson@swansea.ac.uk

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Abstract

1. The development of multisensor animal-attached tags, recording data at high frequencies, has enormous potential in allowing us to define animal behaviour.
2. The high volumes of data, are pushing us towards machine-learning as a powerful option for distilling out behaviours. However, with increasing parallel lines of data, systems become more likely to become processor limited and thereby take appreciable amounts of time to resolve behaviours.
3. We suggest a Boolean approach whereby critical changes in recorded parameters are used as sequential templates with defined flexibility (in both time and degree) to determine individual behavioural elements within a behavioural sequence that, together, makes up a single, defined behaviour.
4. We tested this approach, and compared it to a suite of other behavioural identification methods, on a number of behaviours from tag-equipped animals; sheep grazing, penguins walking, cheetah stalking prey and condors thermalling.
5. Overall behaviour recognition using our new approach was better than most other methods due to; (1) its ability to deal with behavioural variation and (2) the speed with which the task was completed because extraneous data are avoided in the process.
6. We suggest that this approach is a promising way forward in an increasingly data-rich environment and that workers sharing algorithms can provide a powerful library for the benefit of all involved in such work.

KEYWORDS

accelerometer, behaviour, behaviour identification, bioinformatics, software

1 | INTRODUCTION

Animal behaviour has been variously defined, but generally can be defined as “the way in which an animal works, functions or responds to a particular situation” (Tinbergen, 1960) with consequences for lifetime reproductive success (Birkhead, Atkin, & Møller, 1987; Drews, 1993; Krebs & Davies, 2009; Krebs, Davies, & Parr, 1993). As such, our ability to determine animal behaviours precisely is critically important for the proper understanding of animal ecology and ecosystem functioning (Krebs et al., 1993). Indeed, it is this that explains the large variety of methodologies developed to quantify behaviour (e.g. Altmann, 1974; Chastin & Granat, 2010; Lucas & Baras, 2000; Miller & Gerlai, 2007; Tinbergen, 1960). A particularly rapidly developing field in this regard is “biologging” – the deployment of autonomous tags on animals to record data (Hooker, Biuw, McConnell, Miller, & Sparling, 2007). Specifically, the extraordinary development of electronic technology over the last three decades has led the progression of sophisticated miniature sensors coupled with low power consumption and rapidly expanding memory capacity (Ropert-Coudert & Wilson, 2005) so that studies using multisensor technology in tags on animals are now common (Brown, Kays, Wikelski, Wilson, & Klimley, 2013). This has led from the simple animal-attached tags of the 1990s recording data once every few seconds (Wilson, Culik, Bannasch, & Lage, 1994), to systems today that may record multiple channels at thousands of Hertz (Johnson & Tyack, 2003). Of particular note for defining behaviours is the role played by accelerometers, gyroscopes and magnetometers, which can resolve both animal attitude in the three spatial axes (Williams et al., 2017; Yoda et al., 1999) and movement (Fourati, Manamanni, Afilal, & Handrich, 2011; Noda, Kawabata, Arai, Mitamura, & Watanabe, 2014). These are primary elements used in classifying behaviours (Tinbergen, 1960), and so have great potential in studies of wild animals.

However, the ease with which we can now record the physical manifestation of behaviour, *via* metrics such as pitch, roll and “dynamism” in the acceleration signature (Laich, Wilson, Quintana, & Shepard, 2008), is tempered by the difficulties of dealing with the complexity and volume of such data. Thus, computational solutions for processing the signals are inevitable and, accordingly, there is a rich and varied literature dealing with this (e.g. Nathan et al., 2012; Resheff, Rotics, Harel, Spiegel, & Nathan, 2014; Sakamoto et al., 2009). This includes support vector machines (Tachibana, Oosugi, & Okanoya, 2014), regression trees (de Weerd et al., 2015), random forests (Bidder et al., 2014), neural networks (Samarasinghe, 2016), linear discriminant analysis (Anderberg, 2014) and template-matching (Walker, Jones, Laramée, Holton, et al., 2015). Each method has advantages and disadvantages (Resheff et al., 2014) but prime negative issues revolve around subjectivity, whether the data are parametric, the extent of over-fitting, and the computational time involved in the process (Nathan et al., 2012). In addition, a particular weakness of many systems is that they fail to recognise the temporal sequencing of the movements that define the fundamental unit of that behaviour and the variability within them, and thereby preclude an important discriminator. For example, walking may be

defined by a cluster of acceleration metrics (Bidder et al., 2014) but the fundamental unit of walking is the single step (Moe-Nilssen & Helbostad, 2004) and this has well-defined properties over time (Sabatini, Martelloni, Scapellato, & Cavallo, 2005) that could, for example, be used in any decision tree-based approach.

In this paper, we present an approach for identifying behaviours from data derived from animal-attached tags that recognises (1) the lowest common denominator (LoCoD) defining any particular behaviour (i.e. a single step is the lowest common denominator within walking) and (2) that this lowest common denominator can be usefully broken down into base elements (BEs) (such as an increase, followed by a drop, in dorso-ventral acceleration for walking [Rong, Zhiguo, Jianzhong, & Ming, 2007]), all of which have to follow each other in a defined sequence for the LoCoD to be apparent. Finally, (3), the timing of BEs within a sequence is often constrained. Thus, this process provides a recognisable key for LoCoDs of behaviours based on measurements, sequences and timings of BEs. We appreciate that much of the essence of this is inherent in some template-matching approaches (Walker, Jones, Laramée, Bidder, et al., 2015) but combine this with both temporal flexibility across all BEs, together with an ability to switch between and incorporate defined, often derived, metrics that provide critical information for a powerful match. We demonstrate the utility of this approach by using it to search for behaviours that have LoCoD periods ranging between fractions of a second and several minutes using data derived from animal-attached tags and compare it briefly to other computational methods.

2 | MATERIALS AND METHODS

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

2.1 | The LoCoD method

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

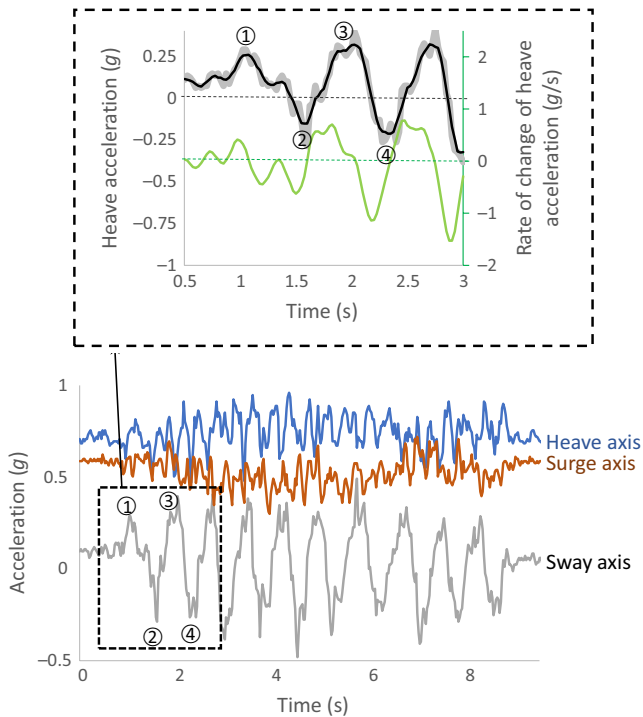


FIGURE 1 Twenty steps (the first four numbered) taken by a Magellanic penguin *Spheniscus magellanicus* during walking on the beach, manifest by triaxial acceleration data at 40 Hz. The bird starts and ends stationary, but begins to walk, with two small steps before rapidly changing to steps with clear waveforms, particularly in the sway (lateral) axis (grey line). Within the LoCoD (lowest common denominator) 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 five 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)

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

$$\text{BE}_1 - \text{RECOGNISE WHEN}; dA_{h_s}/dt > 0.25 \text{ g/s}, \quad (1)$$

where A_{h_s} is the smoothed heave acceleration following;

$$A_{h_s} = \frac{1}{n} \sum_{i=0}^{n-1} A_{h-s} - i \quad (2)$$

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

$$\begin{aligned} \text{BE}_1 - \text{RECOGNISE WHEN}; & dA_{h_s}/dt > 0.25 \text{ g/s} \\ \text{AND}; & dA_s/dt > 0.05 \text{ g/s} \\ \text{AND NOT}; & D > 0m \end{aligned} \quad (3)$$

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

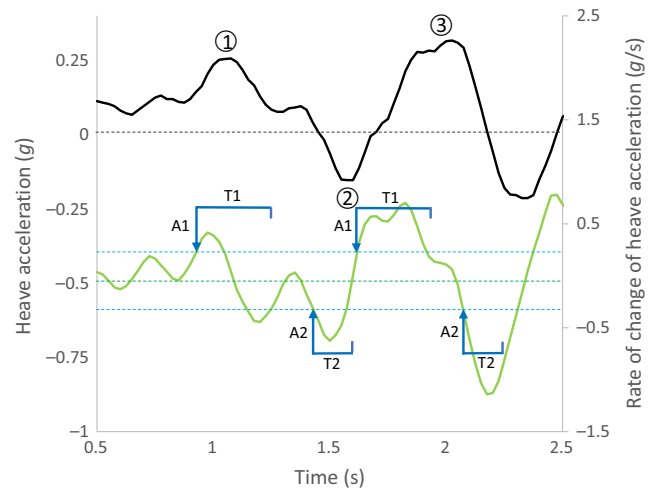


FIGURE 2 The first three steps (numbered) of the walking period shown in Figure 1 for the smoothed heave axis (black line) and the rate of change of the heave axis (green line). The LoCoD (lowest common denominator) method first identifies a feature, or combination of features, that signify the initiation 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 programme 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

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

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

Thus, in the example above, recognition of BE₁ followed by BE₂ to give an LoCoD for one left stride followed by one right stride (Figure 2) could be;

(BE ₁) <i>Presence</i>	WHEN; $dA_{h_s}/dt > 0.25 \text{ g/s}$ FOR $t > 0.2 \text{ s}$ IS TRUE
(BE ₁) <i>Range</i>	SKIP DATA FOR 0.25 s
(BE ₂) <i>Flexibility</i>	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 BE ₁

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

1. be less susceptible to outliers (cf. *Presence*),
2. detect the beginning of a waveform (cf. A1 in Figure 2) and then allows flexibility in time to pass the peak of that waveform (cf. *Range*)
3. constrain the length of time within which the next sub-element must occur for it to be considered part of the LoCoD (cf. *Flexibility*).

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

2.1.1 | Suggestions for defining behavioural elements

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

In order to test the applicability of the LoCoD method over different behavioural periods, we used animal data corresponding to;

1. "Short-period" LoCoDs of behaviours, manifested by actions typically lasting <1 s: The examples used for this study were single bites of sheep and single steps by penguins walking.
2. "Medium-period" LoCoD of behaviours, typically lasting several seconds: The example used here was condors thermalling.
3. "Long-period" LoCoD of behaviours, typically lasting from between 30 s up to minutes: Here, we used cheetahs stalking prey.

A training dataset was created for behavioural identification for each of the above species, where all cases of the given behaviour was identified either according to known instances where the behaviour had been directly observed, or recorded, or by manual identification

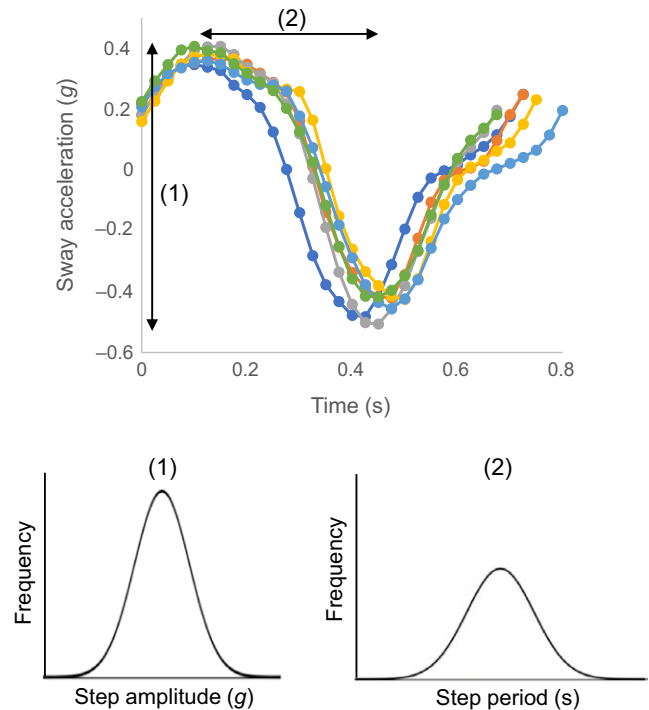


FIGURE 3 Example of the process of defining the value of parameters used to identify behavioural elements in the lowest common denominator (LoCoD) method. The upper graph shows multiple examples of a given behaviour (penguin walking) in a recorded data stream that represents the behaviour well (in this 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

by an expert (see Supplementary material for behaviour descriptions and LoCoD definitions).

The LoCoD method was compared to other methods, see below, by considering the following metrics to assess classification performance: (1) Processing time (in seconds), which is the time spent by our single computer (to ensure that processing capacity was the same for all tasks) to identify and classify behaviours within defined datasets, and (2) Confusion Matrix-based scores: These metrics include Recall and Precision, which are routinely used in such comparisons (Resheff et al., 2014). Recall (also known as Sensitivity or True Positive rate) is estimated as: True Positives/(True Positives + False Negatives); and Precision is estimated as: True Positives/(True Positives + False Negatives). These two metrics are interesting because when Recall values increase, Precision values decrease, and we can assess the performance of a model by focusing the balance between both measures. By calculating both, we have a measure that expresses the ability of the model to find a particular behaviour in the dataset (i.e. Recall) while we have also a measure that expresses the proportion of the data points that our model classified as a particular behaviour

that actually was that behaviour (i.e. Precision). We do not present Accuracy values for two reasons; (1) since the LoCoD method does not consider each data point individually, quantification of the identification result of a given LoCoD case cannot give a true negative result and; (2) although true negative results can be established with the machine-learning methods, Accuracy can give biased results for unbalanced datasets (i.e. when the number of true positives in the confusion matrix is very different to the true negative (Sokolova & Lapalme, 2009; Stapor, 2017).

2.2 | Comparator methods

We compared the outputs of the LoCoD method with nine different behavioural classifier models. These were; (1) *K*-Nearest Neighbours ($K = 3$), (2) Linear Support Vector machines (Linear SVM), (3) Radial Basis Function kernels for Support Vector Machines (RBF SVM), (4) Decision Trees, (5) Random Forest, (6) Naïve Bayes, (7) Linear Discriminant Analysis (LDA), (8) Quadratic Discriminant Analysis (QDA), (9) Artificial Neural Networks (ANN). These are all offered within a single piece of software as freeware (Accelerater, <http://accapp.move-ecol-minerva.huji.ac.il/>) (Resheff et al., 2014) which facilitates protocols and testing (see a brief description of each model in Supplementary material). When using Accelerater, we used the “all features” option to construct the models (selecting the “precomputed stats, Label” option from the upload tab, to ensure that we could have available the same features employed with LoCoD) and a Train-Test split (50% for training and 50% for testing) for validation as for the LoCoD method. We note though, that machine learning methods have numerous options for fine tuning,

which can have an appreciable impact on the overall accuracy (Ladds et al., 2017) so our comparison between machine learning options and the LoCoD method may have disadvantaged the machine learning process.

3 | RESULTS

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

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

For penguin walking, there were four machine-learning algorithms that showed similar performance for all metrics (Nearest

TABLE 1 Performance and time taken for the different identification methods to identify all cases of the “short-period” behaviour of sheep biting and penguin walking in their respective datasets (see supplementary material for further detail). For each method, the time taken for the algorithm to run through the complete dataset is given, along with the measures of recall and precision

Method	Sheep biting			Penguin walking		
	Time (s)	Recall	Precision	Time (s)	Recall	Precision
Manual	2,039	1.00	1.00	2,040	1.00	1.00
LoCoD (lowest common denominator)	1.5	0.89	0.87	14	0.98	0.98
Nearest neighbour	243	0.00	0.00	77	0.97	0.96
Linear support vector machines	3,189	0.00	0.00	359	1.00	0.75
Radial basis function kernels for support vector machines	253	0.00	0.00	79	0.94	0.97
Decision tree	242	0.00	0.00	80	0.97	0.96
Random forest	281	0.00	0.00	82	0.98	0.96
Naïve Bayes	317	0.00	0.00	75	0.99	0.76
Linear discriminant analysis	264	0.00	0.00	74	0.99	0.76
Quadratic discriminant analysis	353	0.99	0.01	77	0.76	0.71
Artificial neural networks	3,451	0.00	0.00	405	0.92	0.97

Values in bold show the performance of the LoCoD method.

Method	Condor thermalling			Cheetah stalking		
	Time (s)	Performance		Time (s)	Performance	
		Recall	Precision		Recall	Precision
Manual	2,220	1.00	1.00	180	1.00	1.00
LoCoD (lowest common denominator)	9	0.87	0.73	7.2	0.89	0.89
Nearest neighbour	2,182	0.14	0.26	4,045	0.99	0.98
Linear support vector machines	NA	NA	NA	NA	NA	NA
Radial basis function kernels for support vector machines	NA	NA	NA	NA	NA	NA
Decision tree	2,358	0.01	0.35	3,470	0.99	0.99
Random forest	2,998	0.00	0.00	4,217	1.00	0.98
Naïve Bayes	NA	NA	NA	3,179	0.19	0.03
Linear discriminant analysis	2,152	0.01	0.01	3,016	0.06	0.26
Quadratic discriminant analysis	2,157	0.54	0.91	NA	NA	NA
Artificial neural networks	NA	NA	NA	NA	NA	NA

Values in bold show the performance of the LoCoD method.

Neighbour, RBF SVM, Decision Tree, and Random Forest). The LoCoD method showed similar performance (Recall and Precision above 95%) but with processing times that were a fraction of the best machine-learning approaches (Table 1).

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

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

Overall, and of particular note, was that the LoCoD method dealt particularly well with behavioural identification where the temporal variability of the behaviour was high (defined by the range in duration of the different base elements of the behaviour). For example, in the case of the condor thermalling, manual labelling showed that

TABLE 2 Performance and time taken for the different identification methods to identify all cases of “medium-period” behaviour, consisting of condor thermalling and the “long-period” behaviour of cheetah stalking in their respective datasets (see supplementary material for further detail). For these two behaviours, a number of machine-learning methods were not run to completion due to some system error, generally after more of 20 hr of processing time (marked with NA). For each method, the time taken for the algorithm to run through the complete dataset is given, along with the measures of recall, and precision

each complete turn had a mean duration of 19.7 ± 4.9 s (SD), showing the variation in the presence, range and flexibility (cf. Figure 3) of the two base elements used to define this behaviour (based on altitude gain and rates of change of magnetometry data - Supplementary Data, Table S3.3). Given that the sum of these three values limits the maximum duration of the LoCoD, all but one of the labelled LoCoD complete turns in thermal soaring were 15 s in duration. Similarly, where the machine-learning methods struggled with identification of the cheetah stalking, the LoCoD method performed well; the temporal range of this behaviour being 48.3 ± 16.2 s.

4 | DISCUSSION

4.1 | Speed vs. accessibility considerations in identifying behaviours

In his seminal work on behaviour, Tinbergen (Tinbergen, 1960) defined behaviours by noting prescribed changes in animal movement over time. This approach gets to the heart of behaviour description and is one that should be accessible by those using animal-attached sensors, e.g. accelerometers, magnetometers and gyroscopes (Johnson & Tyack, 2003), that record body postures and movement in its various forms over time. Indeed, the precision with which movement descriptors such as angular velocity and acceleration can be measured has catalysed many studies of animal behaviour by workers using such smart tags (Yoda et al., 1999). More information about the movement from multiple sensors, many of which measure triaxially to cover the three space dimensions anyway (Johnson &

Tyack, 2003; Wilson, Shepard, & Liebsch, 2008), can lead to very comprehensive descriptions of movement (Yoda, Kohno, & Naito, 2004), something that can be further enhanced by converting primary movement data (such as acceleration) to additional derivatives (such as VeDBA [Qasem et al., 2012]). Interpretation of such diverse and complex data is not intuitive, which makes a good case for machine-learning since no specialised knowledge is required by users. Coupled with this is the expectation that machine-learning systems produce best classifications if they are provided with most data, which makes a clear case for using all possible data (Resheff et al., 2014). However, this brings with it appreciable computational challenges because every new line of information has to be considered computationally with respect to all others. Processing time therefore increases disproportionately with the inclusion of every new data stream (Murphy, 2012). Indeed, although computer processing speed continues to increase roughly according to Moore's Law, so too does our capacity to log data (Schaller, 1997). Our ability to incorporate new sensors within our animal-attached tag systems (Robert-Coudert & Wilson, 2005), coupled with a proclivity to record at ever faster rates (Robert-Coudert & Wilson, 2004) and derive new metrics from the base data (e.g. jerk, static- and dynamic acceleration as well as dynamic body acceleration from raw tri-axial acceleration data [Ydesen et al., 2014]) in tandem with tag deployments that may span months bringing in billions of prime data points, inevitably leads to more extended computing times.

Such a compromise might be more acceptable if the performance of machine-learning approaches was exceptional, but our results show that this is not the case (Tables 1 and 2). Our LoCoD approach requires good understanding and careful inspection of the sensor channels in order to make decisions about which data streams are most useful (and in which combination) to define the behaviour. This therefore requires some degree of specialist knowledge of the sensors used and an appreciable initial investment in time, although we would advocate that any use of sensor-acquired data "blind" is not good practice anyway. Our suggestion is that the LoCoD approach specifically follows a three stage process; (1) where the primary data streams of interest are signal-processed to reduce noise and highlight patterns (e.g. via smoothing) over various scales, (2) where derived data streams, most notably differentials, are calculated for inclusion, if relevant (based on expectations and inspection of the behaviour in question) and (3) where conditions for sequential BEs are defined based on precise patterns in selected data streams with defined time-dependent flexibility for their execution. Such an approach is obviously more onerous for the worker than a machine-based learning technique and may be considered a disadvantage. However, this approach frees up appreciable amounts of computational time (Tables 1 and 2) by directing the machine to deal rapidly with a small fraction of the available data. This is critical for complex behaviours made up of many BEs. In the process, it allows identification of the minutia of behaviour if needed (e.g. left footsteps rather than "walking") which may be important for rare, very short-lived behaviours. Indeed, the LoCoD method specifically identifies the smallest common denominator that defines a behaviour according to the

sequence of BEs, for example, single steps, or pairs of steps, within walking, rather than general walking *per se*. This leads to apparent overkill in that the approach will essentially identify every step during the tagged period, which may be more detail than many need, but steps within a defined time interval of each other can be merged without problem to produce larger bouts of walking if preferred and analysed according to behavioural type. Conversely, identification of slow, single steps, such as occur when herbivores graze, can lead to appreciable displacement over time, so their identification can be important in dead-reckoning approaches for resolving animal movement (Bidder et al., 2015). In addition, the ability to separate, for example, "grazing and walking" from "grazing without walking" should allow workers to recognise sub-behaviours within behaviours, something that is considered by people observing animals (Beker et al., 2010) but which are normally overlooked in tag data (Martiskainen et al., 2009). The LoCoD method performed slightly less well with our example of long-period behaviours than with short- or medium-period behaviours (Tables 1 and 2) making it apparently less useful (although the behaviour was identified in <0.5% of the time taken for the manual or machine-learning approach). Ultimately though, the absolute value of the approach depends on the extent to which the variability of the behaviour can be described by the flexibility of the algorithm used (see above). More work will be needed to determine the extent to which our results for cheetahs stalking are typical of "long-lived" behaviours.

4.2 | Libraries of behaviours and inter-specific interpolation

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

starting point for users wishing to examine the same behaviour in another.

5 | CONCLUSIONS

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

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AUTHORS' CONTRIBUTIONS

R.P.W. and M.D.H. conceived and developed the methodology, with input from all other authors. A.d.V., E.L.C.S., F.Q., J.E.S., D.M.S. and S.L. collected the data. A.d.V. and H.W. tested various datasets with the algorithms and various machine-learning software and all authors contributed critically to the development of, and writing, the manuscript.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.56mh682> (Wilson et al., 2018).

ORCID

Rory P. Wilson  <http://orcid.org/0000-0003-3177-0107>

Hannah Williams  <http://orcid.org/0000-0002-6338-529X>

Sergio Lambertucci  <http://orcid.org/0000-0002-2624-2185>

D. Michael Scantlebury  <http://orcid.org/0000-0001-8327-0556>

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