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RESEARCH ARTICLE

Combined use of two supervised learning algorithms to model sea turtle behaviours from tri-axial acceleration data

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ABSTRACT

Accelerometers are becoming ever more important sensors in animal-attached technology, providing data that allow determination of body posture and movement and thereby helping to elucidate behaviour in animals that are difficult to observe. We sought to validate the identification of sea turtle behaviours from accelerometer signals by deploying tags on the carapace of a juvenile loggerhead (*Caretta caretta*), an adult hawksbill (*Eretmochelys imbricata*) and an adult green turtle (*Chelonia mydas*) at Aquarium La Rochelle, France. We recorded tri-axial acceleration at 50 Hz for each species for a full day while two fixed cameras recorded their behaviours. We identified behaviours from the acceleration data using two different supervised learning algorithms, Random Forest and Classification And Regression Tree (CART), treating the data from the adult animals as separate from the juvenile data. We achieved a global accuracy of 81.30% for the adult hawksbill and green turtle CART model and 71.63% for the juvenile loggerhead, identifying 10 and 12 different behaviours, respectively. Equivalent figures were 86.96% for the adult hawksbill and green turtle Random Forest model and 79.49% for the juvenile loggerhead, for the same behaviours. The use of Random Forest combined with CART algorithms allowed us to understand the decision rules implicated in behaviour discrimination, and thus remove or group together some 'confused' or under-represented behaviours in order to get the most accurate models. This study is the first to validate accelerometer data to identify turtle behaviours and the approach can now be tested on other captive sea turtle species.

KEY WORDS: Accelerometry, Endangered species, Supervised learning algorithms

INTRODUCTION

The study of animal behaviour has historically been limited by the difficulty of observing individuals in the wild, and also because human presence can change animal behaviour (Schneirla, 1950; Jack

et al., 2008). In fact, direct observation is often considered impossible in far-ranging, shy or nocturnal species. These limitations have, in part, catalysed the development of 'biotelemetry', where study animals wear systems that transmit data to remote receiving stations (Cagnacci et al., 2010; Tomkiewicz et al., 2010). Such systems can help researchers determine animal location, and therefore space use, and movement without bias due to disturbance related to human observation (Kooyman, 2003; Hart and Hyrenbach, 2010; Hubel et al., 2016). Beyond this, when treated with state-space models, location data can also lead to powerful inferences relating to behaviour (Chevallier et al., 2010; Dodge et al., 2014; Chambault et al., 2015, 2017). A development over the last 20 years, however, has been the use of tag-linked accelerometers, which can be used to produce a recording of the change in body velocity, and this has proven particularly powerful in providing data that enable us to elucidate animal behaviour over temporal scales of seconds (Yoda et al., 1999; Shepard et al., 2008; Brown et al., 2013). Indeed, many now regard the use of accelerometers in animal-attached tags as pivotal in allowing us to understand how animals change behaviour as a function of space (Narazaki et al., 2009) and time (Watanabe et al., 2004, 2012; Fossette et al., 2012; Shamoun-Baranes et al., 2012), a concept that was considered impossible just three decades ago.

Sea turtles are long-distance migrants, with some travelling several thousand kilometres from their nesting sites to their foraging grounds (Spotila, 2004; Baudouin et al., 2015; Chambault et al., 2017). This lifestyle, which also involves them exploiting considerable depths (leatherback sea turtles, *Dermochelys coriacea*, may dive to depths in excess of 1230 m; Spotila, 2004), makes visual observation problematic. Given that some sea turtle populations are subject to substantial anthropogenic pressures, with drastic declines being apparent in six of the seven extant species (International Union for Conservation Nature, 2018), any information pertaining to their ecology is valuable. Indeed, the expectation is that high-resolution behavioural data, especially those linked to habitat, could be pivotal in making informed conservation decisions (Baudouin et al., 2015).

In this context, accelerometers have been used to identify and classify different animal behaviours (Brown et al., 2013; Collins et al., 2015; Graf et al., 2015). However, to our knowledge, only a limited number of studies have examined sea turtle behaviour using accelerometric data. For example, turtle feeding and breathing behaviours have been well described by accelerometers placed on the lower beaks (Okuyama et al., 2009), although normally acceleration loggers are attached to the turtle shell. Signals from these tags have allowed researchers to study turtle energy expenditure in relation to diving (Enstipp et al., 2011; Fossette et al., 2012), and have also been used in general descriptions of behaviours (Hochscheid et al., 1999; Yasuda and Arai, 2009; Fossette et al., 2010). However, as the accelerometric signals used in these studies to identify sea turtle behaviours in water were not

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validated by simultaneous observation of the tag-equipped animals, there is room for significant bias in the interpretation of the results.

In this experimental study, we examined how behaviours observed in three species of sea turtle (*Chelonia mydas*, *Eretmochelys imbricata* and *Caretta caretta*), living in captivity, relate to the signals from tri-axial accelerometers incorporated into turtle-attached tags.

This study should provide tools for scientists in future studies to determine turtle behaviour with greater confidence and constitutes an important step in defining the behaviours and ecological needs of these enigmatic animals. The ultimate aspiration is that this will help inform conservation decisions.

MATERIALS AND METHODS

Data collection

The study was carried out in February 2015 at Aquarium La Rochelle, France. Tri-axial accelerometers [Wilog Acquisition Control Unit (WACU), size 21×13×4 mm, mass 2 g; conceived, built and calibrated by the Métrologie et Instrumentation Biologie et Environnement (MIBE) team, CNRS-IPHC, Strasbourg, France] were attached to three species of sea turtle: one adult green turtle, *Chelonia mydas* (Linnaeus 1758) [mass 58.60 kg, straight carapace length (SCL) 72.50 cm, curved carapace length (CCL) 76.00 cm], one adult hawksbill turtle, *Eretmochelys imbricata* (Linnaeus 1766) (mass 58.30 kg, SCL 70.90 cm, CCL 74.00 cm) and one juvenile loggerhead turtle, *Caretta caretta* (Linnaeus 1758) (mass 9.23 kg, SCL 39.60 cm, CCL 43.00 cm). The green turtle and the hawksbill were held in the same tank with a water volume of 150 m³ (7 m length×5.6 m width×4.1 m depth) while the loggerhead was in a separate tank of 56 m³ (5.6 m length×4.8 m width×2.5 m depth). Each WACU recorded acceleration at 50 Hz in each of the three orthogonal axes of the animal: the anterior–posterior axis (AccX, surge), the lateral axis (AccY, sway) and the dorso-ventral axis (AccZ, heave) (Fig. 1). In addition to acceleration, pressure, luminosity and temperature were measured at 1 Hz. Each WACU was placed in a structure attached to the turtle carapace using waterproof double-backed adhesive tape (Fig. 1). Data collection lasted 1 day per individual; turtles were caught and equipped the morning before the Aquarium La Rochelle opened and then released

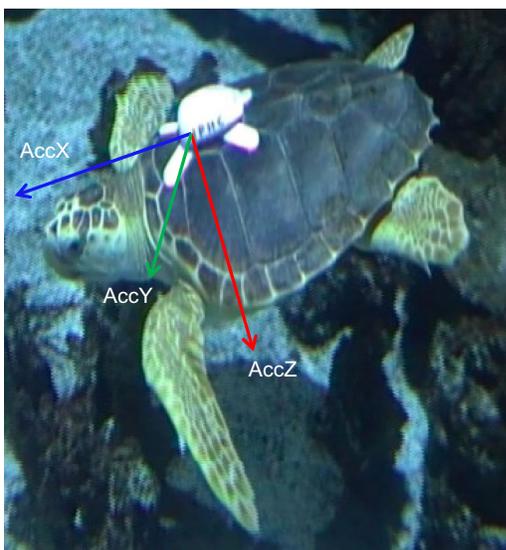


Fig. 1. Accelerometer attachment. A captive loggerhead turtle equipped with a bio-logger (WACU) attached to the carapace using waterproof double-backed adhesive tape. The three arrows indicate the axes measured by the accelerometers.

into their respective tanks. During the day, two fixed cameras (Sony and JVC) were placed to record turtle behaviours, while a third (Samsung) was used spontaneously by an operator for detailed documentation of particular behaviours such as food intake. Devices were removed from the turtles at the end of the day.

Identification of behaviours

Videos were manipulated using Kinovea software (Association Kinovea 2015). A shared ethogram of the three sea turtles was derived following a preliminary video analysis (Table 1). All labelled behaviours were placed into one of 10 categories: ‘breathing’, ‘feeding on prey’ (termed ‘prey’ hereafter), ‘flipper-beating without translocation’ (termed ‘swimming in place’ hereafter), ‘grazing’, ‘half-immersed’, ‘interaction’, ‘resting’, ‘swimming horizontally’, ‘U-turn’ and ‘vertical transition’. The sea turtles were fed once during the experiment with hake fillets, sardines, prawns and lettuce distributed at the surface. The behavioural category ‘prey’ was intended to simulate normal feeding. ‘Grazing’ was used when a turtle was apparently looking for plant food on the rocks of the tank. The category ‘interaction’ included the social behaviours expressed between the hawksbill and the green turtle. Some of the categories were subdivided according to the inclination of turtle body (e.g. horizontal versus vertical; Table 1). Footage was time stamped manually to allow further synchronization with sensor data (e.g. acceleration, pressure).

The loggerhead exhibited movements in different proportions to those of the hawksbill and green turtle. For this reason, two different models were constructed.

Acceleration data analysis

Tri-axial acceleration data were downloaded from the loggers by the MIBE team (CNRS-IPHC). Acceleration data analysis required several calculations in order to obtain the variables needed for behaviour discrimination. These calculations were made using custom-written scripts (Y.H. and M.-A.F.-W.).

The raw acceleration data (Acc) recorded by the logger are considered to have two components: the static acceleration (St) due to the gravity and the dynamic body acceleration (DBA) stemming from the movement of the animal (Shepard et al., 2008; Wilson et al., 2008; Brown et al., 2013). For the three different axes (*x*, *y* and *z*) these can be summarized as;

$$\text{AccX} = \text{StX} + \text{DBAX}, \quad (1)$$

$$\text{AccY} = \text{StY} + \text{DBAY}, \quad (2)$$

$$\text{AccZ} = \text{StZ} + \text{DBAZ}. \quad (3)$$

The static acceleration was isolated by subjecting the raw acceleration to a low-pass Butterworth filter (Matlab function ‘filtfilt’, using a threshold of 0.8 s) (Willener et al., 2015). The resulting data were then used to derive the body pitch angle (pitch) and roll angle (roll) using the following equations (Wilson et al., 2008; Collins et al., 2015; Willener et al., 2015; Wilson et al., 2008; Forin-Wiart et al., 2014; Collins et al., 2015):

$$\text{Pitch} = \arcsin\left(\frac{-\text{StX}}{\sqrt{\text{StX}^2 + \text{StY}^2 + \text{StZ}^2}}\right) \times \frac{180}{\pi}, \quad (4)$$

$$\text{Roll} = 2 \arctan\left(\frac{\text{StZ}}{\text{StY} + \sqrt{\text{StY}^2 + \text{StZ}^2}}\right) \times \frac{180}{\pi}. \quad (5)$$

The dynamic acceleration was obtained by subtracting the static acceleration from the raw acceleration. A proxy for energy

Table 1. Shared ethogram of the three turtles

Behavioural category	Behaviour	Description
Breathing		Turtle is breathing at the surface.
Grazing (G)	G downward	Turtle is 'looking for food' around the rocks, giving the impression of grazing.
	G upward	Turtle is grazing with the head lower than the rear of the body.
	G hori	Turtle is grazing with the head higher than the rear of the body. Turtle is grazing with the head in line with the rear of the body.
Half-immersed		The half of the turtle body is out of the water.
Interaction (INT)	INT victim	Turtle is aggressed by a second turtle.
	INT peck	Turtle is executing head lunges at a second turtle.
	INT escape	Turtle is escaping to avoid aggression from another turtle.
	INT pursuit	Turtle is pursuing a second turtle.
Prey		Turtle is opening its beak to feed.
Resting (R)	RB upward	Turtle is resting at the bottom of the tank with the body front tilted slightly down.
	RB hori	Turtle is resting at the bottom of the tank with the body held horizontally.
	RR downward	Turtle is stuck between two rocks with the head lower than the rear of the body.
	RR upward	Turtle is stuck between two rocks with the head higher than the rear of the body.
	RR hori	Turtle is stuck between two rocks with the body horizontal.
Swimming horizontally (SH)	SH downward	Turtle is swimming horizontally with the head lower than the rear of the body.
	SH upward	Turtle is swimming horizontally with the head higher than the rear of the body.
	SH hori	Turtle is swimming horizontally with the body positioned horizontally.
Swimming in place (SIP)		Turtle is swimming actively in order to hold its position in the water column.
	SIP downward	Turtle is swimming in place, keeping its head lower than the rear of its body.
	SIP upward	Turtle is swimming in place, keeping its head higher than the rear of its body.
U-turn		Turtle is executing a 180 deg turn.
Vertical transition (VT)		Movement upward and/or downward.
	AVTB downward	Turtle is swimming actively toward the bottom with the head lower than the rear of its body
	AVTB upward	Turtle is swimming actively toward the bottom with its head higher than the rear of its body.
	AVTS downward	Turtle is swimming actively toward the surface with its head lower than the rear of its body.
	AVTS upward	Turtle is swimming actively toward the surface with its head higher than the rear of its body.
	PVTB	Turtle is swimming passively towards the bottom with the body pitch parallel to its trajectory.
	PVTB drift	Turtle is swimming passively towards the surface with the body pitch not parallel to its trajectory.
	PVTS	Turtle is swimming passively towards the bottom with the body pitch parallel to its trajectory.
	PVTS drift	Turtle is swimming passively towards the surface with the body pitch not parallel to its trajectory.
	VTB window	Turtle is swimming towards the bottom, with its carapace against the window.
	VTS window	Turtle is swimming towards the surface, with its belly against the window.

expenditure (metabolic power), called overall dynamic body acceleration (ODBA), can be obtained by summing the absolute values of dynamic acceleration across the three axes (Wilson et al., 2006; Gleiss et al., 2011; Halsey et al., 2011). Halsey et al. (2011) showed that ODBA was a reliable indicator of the overall energy expenditure of sea turtles. More recently, a similar indicator was proposed, vectorial dynamic body acceleration (VeDBA) (Walker et al., 2015), which represents the vectorial sum of the dynamic body acceleration:

$$\text{VeDBA} = \sqrt{\text{DBAX}^2 + \text{DBAY}^2 + \text{DBAZ}^2}. \quad (6)$$

ODBA and VeDBA are both reliable indicators of oxygen consumption and thus energy expenditure, and are tightly correlated (Qasem et al., 2012). In this study, we used VeDBA, which is less susceptible to errors in the variation of the angle at which the tag is placed on the animal (Qasem et al., 2012). Thus, we extracted nine variables from the raw acceleration data (StX, StY, StZ, DBAX, DBAY, DBAZ, pitch, roll and VeDBA) (Fig. 2).

Time matching and labelled dataset

The various behaviours obtained from the video analysis were synchronized with the accelerometer data using time-specific calibrations (a defined repetitive motion was performed on each accelerometer at a precise time at the beginning and end of the experiment). The behavioural sequences were then cut into segments. The behaviours 'prey', 'breathing' and 'interaction', were termed 'brief behaviours', because they were performed rapidly and apparently opportunistically by the turtles. Accordingly, 'brief behaviours' were cut into segments of 2 s (this period corresponded to our observation of the minimum execution time). In contrast, the time step of the 'long behaviours' corresponded to the mean time taken for the study turtles to execute two flipper beats, and thus effectively represent the beat frequency. In order to determine this explicitly, 20 sequences of each of the 'long behaviours' were randomly selected and analysed to measure the time corresponding to two flipper beats. A mean was obtained from these measures for each turtle. Thus, the sequences of 'long behaviours' were divided into 6 s segments for the green and

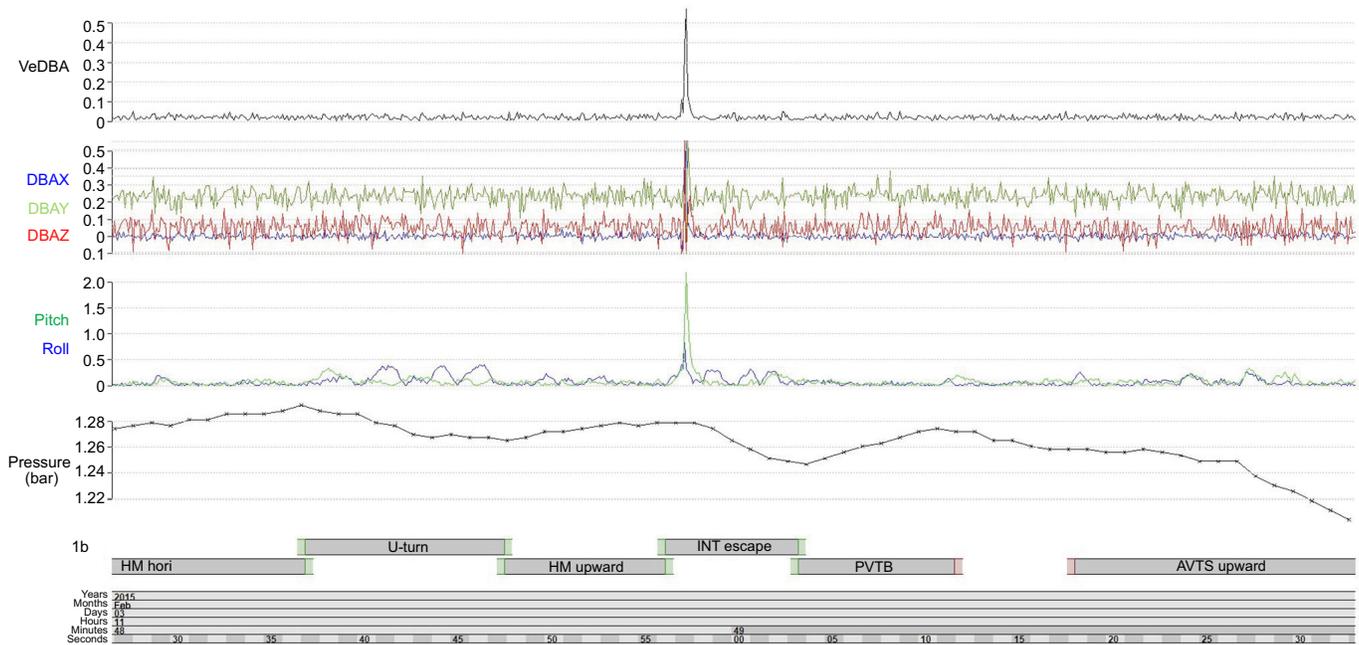


Fig. 2. Accelerometer and pressure data from the tag attached to the green turtle. Vectorial dynamic body acceleration (VeDBA) and dynamic body acceleration (DBA) variables in the *x*-, *y*- and *z*-direction (DBAX, DBAY and DBAZ; **g**) were extracted from the raw acceleration data, and the body pitch angle and roll angle (deg) were calculated from the static acceleration data. For definitions of behaviours in the lower panel (HM, INT, PVTB, AVTS), see Table 1.

hawksbill turtles and 4 s segments for the loggerhead turtle. In order to describe the labelled behaviours precisely, descriptive statistics (means, minimum values, maximum values, ranges, variances and standard deviations) were computed from the extracted segments over 2, 4 or 6 s for the nine acceleration-derived variables using the software R version 3.3.1 (R Core Team 2016). In addition, the difference between the pressure at the beginning and at the end of the segment was calculated ('Diff_Deep') as well as the variance, the range and the standard deviation of the pressure. Thus, every behavioural segment was described by 57 variables. The two datasets (one for the green and hawksbill turtles and one for the loggerhead turtle) were subdivided so that 70% was used as a training dataset and 30% was used as a validation dataset (Nathan et al., 2012).

Classification And Regression Tree (CART) and Random Forest modelling

Supervised learning algorithms typically use descriptive variables in order to discriminate behaviours. Among the most used supervised algorithms, Random Forest was shown to be the most accurate for classifying different behaviours from accelerometer data (Nathan et al., 2012). However, it is difficult to determine and interpret the precise decision rules used to classify behaviour as many distinct decision trees are built by the model based on the CART method (Nathan et al., 2012). We thus decided to first use a CART approach (Breiman et al., 1984; R package *rpart*) and then a Random Forest approach (Breiman, 2001; R package *randomForest*, $n=500$ trees, $mtry=28$). This is because the first algorithm displays the decision rules and highlights inconsistencies and this information can be used to improve the Random Forest model.

A confusion matrix was constructed from the test sample showing the well-identified behaviours (true positive, TP, and true negative, TN) and those considered misclassified (false negative, FN and false positive, FP). Three indices were calculated from the matrix to

test the accuracy and the sensitivity of each model (Powers, 2007), given by:

$$\text{Recall} = \frac{TP}{TP + FN}, \quad (7)$$

$$\text{Precision} = \frac{TP}{TP + FP}, \quad (8)$$

$$\text{Accuracy} = \frac{TP + TN}{TP + TN + FP + FN}. \quad (9)$$

RESULTS

Thirty-one different behaviours were identified and ranked into 10 different categories defined in the ethogram (Table 1) in the first analysis. In total, 22 h 47 min of recorded videos were analysed and 2922 behavioural sequences were identified for the three turtles.

Hawksbill and green turtle models

Video analysis

In total, 1842 sequences were identified during 850 min of video analysis; 77.28% of the analysed time was characterized by one of the defined behaviours, which represented 656.92 min (referred to as 'total identified time', TIT). Among the 30 behaviours exhibited by the hawksbill and green turtles, the resting behaviours 'RR hori' and 'RR downward' comprised most of the time (20.06% and 19.21% of TIT, respectively) (Table 2), with the hawksbill spending 71.57% of its TIT asleep compared with only 13% for the green turtle. However, the most commonly observed active behaviours were active vertical transition towards the surface ('AVTS upward') and horizontal movement ('SH hori') (comprising 8.99% and 8.46% of TIT for the adult turtles, respectively).

In order to build the models, behaviours expressed for less than 3% of TIT were considered to be under-represented and were removed from the analysis. These behaviours included 'G downward', 'G hori', 'SH downward', 'SIP downward', 'SIP

upward', 'prey', 'AVTB upward', 'AVTS downward', 'PVTB', 'PVTB drift', 'PVTS', 'PVTS drift', 'VTB window' and 'VTS window'. Similar resting behaviours were grouped together in order to increase their representation: these were 'RB upward' and 'RB hori', grouped as 'RB' (resting on the bottom), and 'RR upward' and 'RR hori', grouped as 'RR' (resting between the rocks). Similarly, the four interaction behaviours were grouped under 'Interaction' ('INT') to facilitate recognition of general interaction behaviours. Considered as 'brief behaviours', the number of sequences of 'interaction' and 'breathing' (which were 46 and 143, respectively) associated with a 2 s window allowed us to keep both behaviours for the models.

The first tests of the model building highlighted the inability of the CART algorithms to discriminate 'U-turn' (recall and precision both <20%) and 'SH upward' (recall <30%). The latter was mostly exhibited by the green turtle before the food was distributed and was considered unnatural anyway. In order to get the most accurate models, both these behaviours were discarded.

Finally, 1055 sequences of 6 different behavioural categories were used to build the models with a time window of 2 s for 'breathing' and 'interaction' and 6 s for all others. We obtained 4469 segments in total: 227 associated with the category 'grazing', 501 with 'swimming horizontally', 171 with 'interaction', 176 with 'breathing', 2796 with 'resting' and 598 with 'vertical transition'. In order to balance the sample used by the algorithms, the number of segments of over-expressed behaviours had to be limited. Following preliminary tests, we found that 350 segments chosen randomly from the over-expressed behaviours gave the best outcome.

CART model

A decision tree discriminating 10 behaviours ('AVTB downward', 'AVTS upward', 'breathing', 'G upward', 'SH downward', 'SH hori', 'interaction', 'RB', 'RR downward', 'RR') from 6 different categories was constructed using the CART method (Fig. 3). The decision tree was relatively easy to understand, with resting

behaviours being discriminated within the first level (Fig. 3). 'RR' was characterized by the low range of StY variables while 'RB' was discriminated from the active behaviours by the low standard deviation of the pitch variable (Fig. 3). For the active behaviours, the mean of the StX variable was important in discrimination of posture (either 'upward-facing' or 'downward-facing') while the difference in pressure ('Diff_Deep') provided information about the nature of the movement (whether vertical or horizontal). The sign of the 'Diff_Deep' also indicated whether the vertical movement was directed towards the surface or the bottom.

The associated confusion matrix indicated a global accuracy of 81.30% (Table S1). The recall index varied from 48.98% to 97.14% and the precision index from 47.06% to 99.03% (Fig. 4A). All resting behaviours were well identified by the model, with 'RR downward' having the highest recall and precision indices. By contrast, the model struggled to discriminate 'breathing' and 'interaction', as manifest in their low recall and precision indices. 'Breathing' had the lowest recall and precision indices, due mainly to confusion with 'G upward' (Table S1).

Random Forest model

The Random Forest model was built using the same behaviours employed in the CART model. As this algorithm tested 28 variables randomly sampled at each split (mtry=28), we took the first 28 most important variables to construct the model (Fig. 5A). The variables associated with pressure were the most important for discriminating turtle behaviours in the Random Forest model, with 'Diff_Deep' being notably discerning. The mean of the StX variable, which defined the different turtle postures (upward-facing and downward-facing), was also particularly discerning, while the dynamic acceleration variable 'min_VEDBA' was the fourth most important variable for discriminating behaviours.

The global accuracy for the discrimination of the 10 behaviours ('AVTB downward', 'AVTS upward', 'breathing', 'G upward', 'SH downward', 'SH hori', 'interaction', 'RB', 'RR downward', 'RR')

Table 2. Number of hawksbill and green turtle behavioural sequences

Conserved behaviours				Grouped behaviours				Discarded behaviours			
Category	Behaviour	Sequence no.	% TIT	Category	Behaviour	Sequence no.	% TIT	Category	Behaviour	Sequence no.	% TIT
Breathing	Breathing	143	1.34	Interaction	INT	46	0.92	Grazing	G downward	34	1.44
Grazing	G upward	86	4.35		INT victim	9	0.16		G hori	29	0.88
Resting	RR downward	14	19.21		INT peck	15	0.27	Prey	Prey	10	0.3
Swimming	SH downward	90	3.22		INT escape	12	0.31	Swimming in place	SIP downward	41	1.66
Swimming horizontally	SH hori	262	8.46		INT pursuit	10	0.18		SIP upward	23	0.78
Vertical transition	AVTB downward	113	3.55	Resting	RB	12	6.29	Swimming horizontally	SH upward	211	6.57
	AVTS upward	280	8.99		RB upward	8	5.72	U-turn	U-turn	242	5.95
					RB hori	4	0.57	Vertical transition	AVTB upward	88	2.9
					RR	9	20.08		AVTS downward	11	0.32
					RR upward	1	0.02		PVTB	47	1.34
					RR hori	8	20.06		PVTB drift	25	0.81
									PVTS	17	0.4
									PVTS drift	6	0.13
									VTB window	1	0.05
									VTS window	2	0.07

Behaviours with percentage of the total identified time (% TIT) >3% were conserved for modelling and are shown in the 'Conserved behaviours' column. Behaviours with % TIT <3% were removed from further analysis (although they are shown in the 'Discarded behaviours' column). Similar under-represented behaviours were grouped together in order to keep them in the analysis (shown in the 'Grouped behaviours' column; bold indicates the grouped data). 'Breathing' and 'INT', highlighted in orange, were 'brief behaviours' and their number of sequences associated with a 2 s window allowed us to keep them in the models. Behaviours highlighted in dark grey showed recall or/and precision indices that were too small in first tests and were therefore discarded from the final model. Light grey indicates discarded behaviors; blue and green indicate grouping of behaviours.

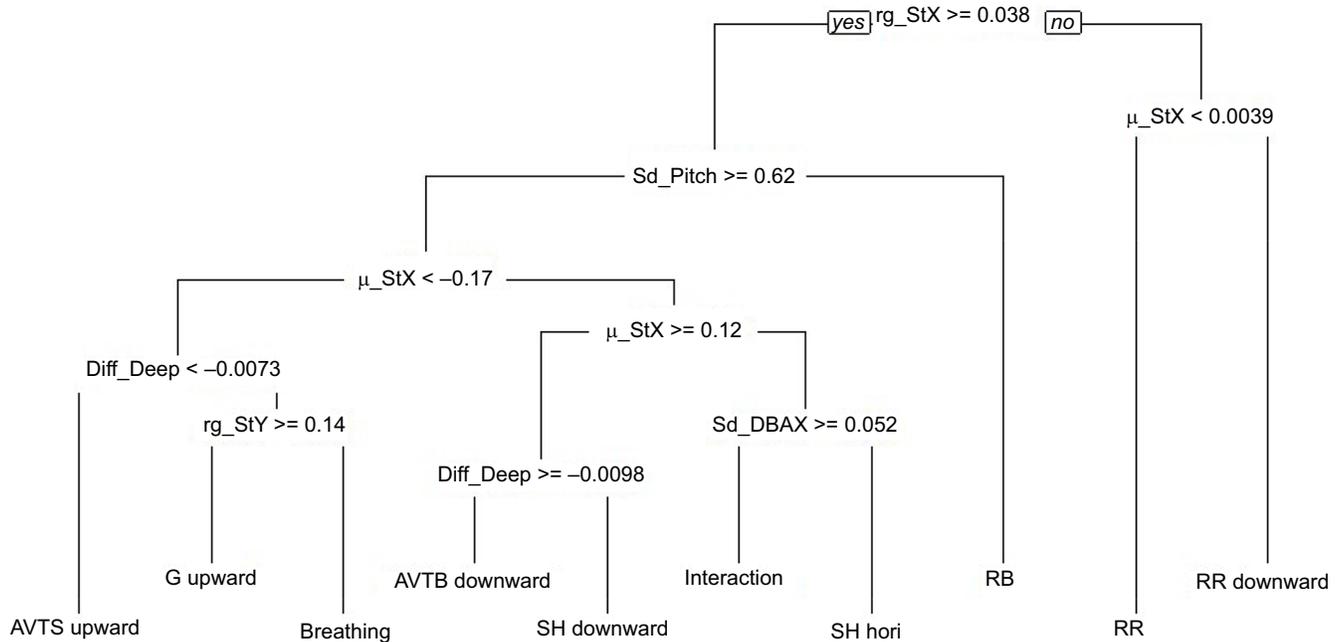


Fig. 3. Decision tree built from the Classification And Regression Tree (CART) algorithm, discriminating 10 behaviours of the hawksbill and green turtles. See Table 1 for explanation of terms. μ , mean; sd, standard deviation; rg, range.

was 86.96% (Table S2). All the precision indices obtained from the CART algorithm were improved in the Random Forest model except for 'AVTB downward' and 'RB', both of which showed a slight decrease (Fig. 4B). The lowest recall index occurred for 'interaction' (70.21%) while 'breathing' had the lowest precision index (71.25%). As with the CART algorithm, inactive behaviours had the highest precision and recall indices.

Loggerhead turtle models

Video analysis

In total, 517 min of recorded video was analysed and 927 behavioural sequences were identified with a TIT of 212.56 min (41.11% of the analysed time). The loggerhead executed 22 behaviours, with 'AVTB downward', 'RB hori' and 'SH downward' being the most common (comprising 20.41%, 15.36% and 15.32% of TIT, respectively) (Table 3). All behaviours that

accounted for more than 3% of TIT were maintained for the models. As with the hawksbill and green turtle models, 'breathing' was kept within the model (see above). The first test of the CART model returned a very low recall value (<30%) for 'SH hori'. In order to get the most accurate models, we decided to exclude this behaviour from the final model to leave 12 behaviours ('AVTB downward', 'AVTS upward', 'Breathing', 'G upward', 'Half-immersed', 'SH downward', 'prey', 'RB hori', 'RR hori', 'U-turn', 'VTB window' and 'VTS window').

We had 739 behavioural sequences, which were cut into 2 s sections for 'prey' and 'breathing' and 4 s sections for the others. We then obtained 2111 segments: 66 placed in the category 'breathing', 86 in 'grazing', 97 in 'half-immersed', 408 in 'swimming horizontally', 91 in 'prey', 563 in 'resting', 107 in 'U-turn' and 693 in 'vertical transition'; 110 segments were chosen randomly from the over-expressed behaviours (see above).

Table 3. Number of loggerhead turtle behavioural sequences

Conserved behaviours				Discarded behaviours			
Category	Behaviour	Sequence no.	% of TIT	Category	Behaviour	Sequence no.	% of TIT
Breathing	Breathing	66	2.22	Grazing	G downward	17	2.06
Grazing	G upward	15	3.75	Grazing	G hori	19	2.67
Half-immersed	Half-immersed	14	3.55	Swimming horizontally	SH hori	43	3.33
Prey	Prey	9	3.72	Swimming in place	SIP downward	31	2.09
Resting	RB hori	4	15.36	Swimming in place	SIP upward	5	0.3
	RR hori	1	3.59	Vertical transition	AVTS downward	44	2.95
Swimming horizontally	SH downward	169	15.32	Vertical transition	PVTB	3	0.22
U-turn	U-turn	84	4.45	Vertical transition	PVTB drift	1	0.04
Vertical transition	AVTB downward	180	20.41	Vertical transition	PVTS	9	0.47
	AVTS upward	65	4.49	Vertical transition	PVTS drift	16	0.84
	VTB window	47	4.59				
	VTS window	85	4.45				

Behaviours with percentage of the total identified time (% TIT) >3% were conserved for modelling and are shown in the 'Conserved behaviours' column. Behaviours with % TIT <3% were removed from further analysis (shown in the 'Discarded behaviours' column). 'Breathing' and 'prey', highlighted in orange, were 'brief behaviours' and their number of sequences associated with a 2 s window allowed us to keep them in the models. Behaviours highlighted in dark grey showed recall indices that were too small in first tests and were therefore discarded from the final model. Orange indicates brief behaviors; light grey indicates discarded behaviors.

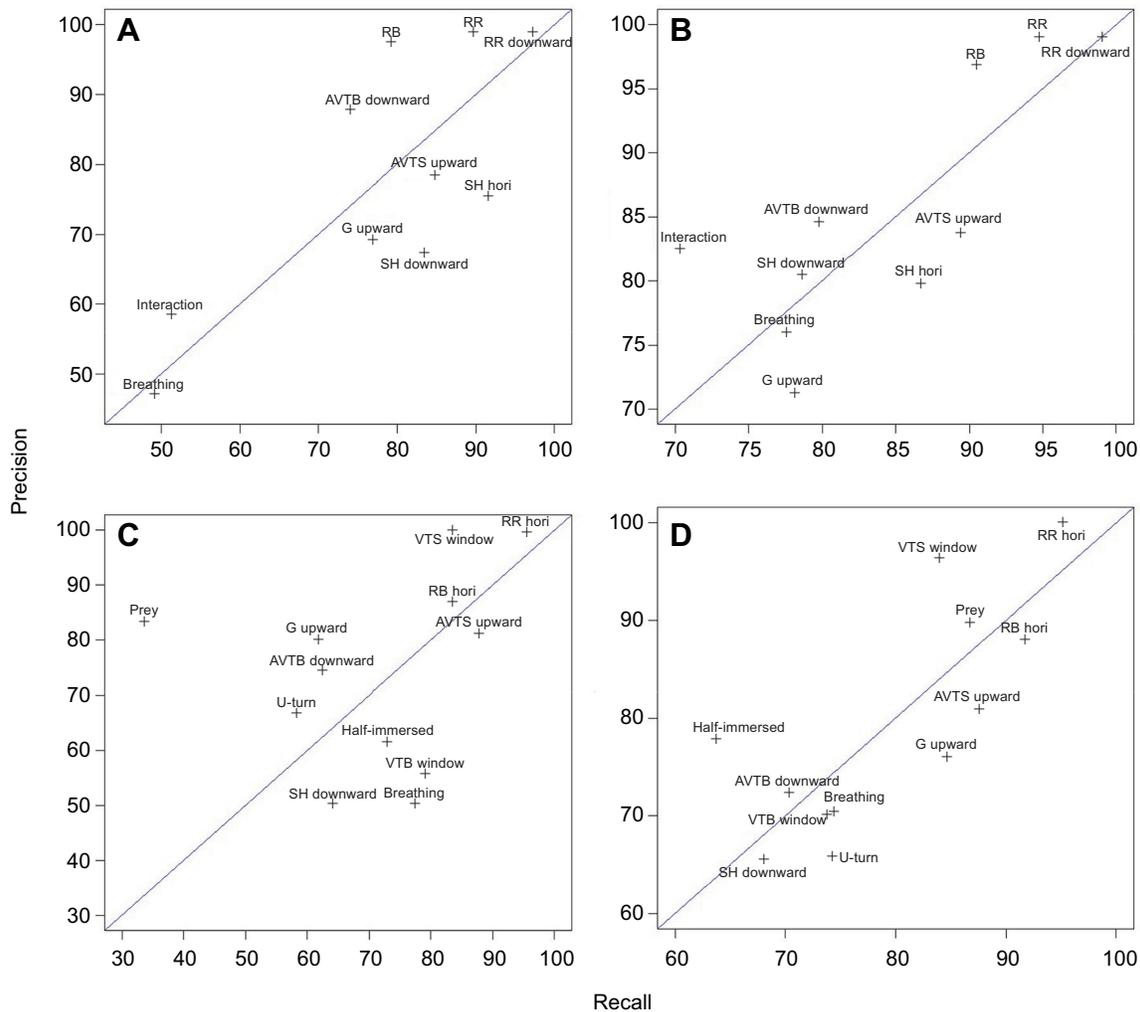


Fig. 4. Plot of precision indices versus recall indices. (A) Plot obtained with the CART algorithm for 10 behaviours of the hawksbill and green turtles. (B) Plot obtained with the Random Forest algorithm for 10 behaviours of the hawksbill and the green turtles. (C) Plot obtained with the CART algorithm for 12 behaviours of the loggerhead turtle. (D) Plot obtained with the Random Forest algorithm for 12 behaviours of the loggerhead turtle. See Table 1 for explanation of terms.

CART model

The decision tree built using the CART method discriminated 12 behaviours ('AVTB downward', 'AVTS upward', 'breathing', 'G upward', 'Half-immersed', 'SH downward', 'prey', 'RB hori', 'RR hori', 'U-turn', 'VTB window' and 'VTS window'). Resting behaviours were the first to be discriminated from the active behaviours by a low range of the StY variable (Fig. 6). Following this, the algorithm identified the vertical transitions towards the surface due to a negative 'Diff_Deep', while movements in the opposite direction were characterized by a positive 'Diff_Deep' value. 'VTB window' differentiated itself from 'AVTB downward' by the higher standard deviation in the DBAY variable. The discrimination of the other categories by the algorithm involved several decision rules based on the static acceleration variables. Only 'SH downward' and 'prey' were separated from one another by the standard deviation of the DBAX variable.

The global accuracy of this model was 71.63% (Table S3). The behaviours identified from the second and third level of discrimination in the CART decision tree ('RR hori', 'RB hori' and 'VTS window') had the highest recall and precision indices

(Fig. 4C). Several 'prey' segments were identified wrongly as 'breathing', leading to a very low 'prey' recall index (33.33%) and a poor 'breathing' precision index (50.00%) (Table S3).

Random Forest model

A Random Forest model was constructed using the 12 highlighted behaviours ('AVTB downward', 'AVTS upward', 'breathing', 'G upward', 'Half-immersed', 'SH downward', 'prey', 'RB hori', 'RR hori', 'U-turn', 'VTB window' and 'VTS window').

'Diff_Deep' was the most important variable used to build the model (Fig. 5B). The mean, the minimum and the maximum of both pitch and StX appeared within the 8 most important variables. The first variable associated with dynamic acceleration ('var_DBAX') was the 14th most important variable in the model.

The loggerhead Random Forest model was associated with a global accuracy of 79.49% (Table S4). 'RR hori' and 'VTS window' had the highest recall and precision indices (Fig. 4D). The identification of 'prey' was significantly increased, with a precision index of 89.66% and a recall index of 86.67%. 'Half-immersed' had the lowest recall index (63.64%) while 'SH downward' had the lowest precision index (65.38%).

global accuracy of 86.96% for the hawksbill and green turtle model and 79.49% for the loggerhead turtle model, demonstrate the value of this approach. Few studies have used the Random Forest algorithm to discriminate behaviours from accelerometer data despite its convincing results. For example, Casale et al. (2011) reported 94.00% accuracy for five behaviours in humans, Resheff et al. (2014) reported 84.02% accuracy for six behaviours in griffon vultures, Graf et al. (2015) reported 94.99% accuracy for six behaviours in Eurasian beavers, *Castor fiber*, and Nathan et al. (2012) reported 90.88% accuracy for seven behaviours in griffon vultures.

As in previous comparative studies (Nathan et al., 2012; Ellis et al., 2014; Resheff et al., 2014; Ladds et al., 2017), the Random Forest algorithm performed better than the CART algorithm, with specific improvement being manifest in the precision and recall indices of the behaviours: here, the global accuracy was 5.66 points higher with the Random Forest algorithm in the hawksbill and green turtle model, and 7.2 points higher in the loggerhead turtle model. In both cases, the behaviours that showed some difficulty in identification by the CART algorithm were associated with a greater increase of one, or both, of the indices in the Random Forest model. In fact, with the exception of the 'SH downward' behaviour in the loggerhead turtle model, these behaviours had the smallest number of segments available for analysis. However, the use of several decision trees by the Random Forest algorithm allowed us to compensate for such low representation, increasing the precision of the model to identify them.

In this study, we used the CART algorithm as a first step in order to understand the main decision rules for identifying behaviours. In fact, the variables that emerged from the CART decision tree were also the first 10 most important variables used to build the random forest model. Of particular note is that the inactive behaviours (within the category 'resting') were rapidly discriminated using two or three decision rules based on static acceleration variables or posture-related parameters (see Fehlmann et al., 2017). This contrasts with other studies that have noted the value of dynamic acceleration (in some ways the polar opposite of static acceleration) in differentiating inactive from active behaviours (Shamoun-Baranes et al., 2012; Soltis et al., 2016). With specific regard to active locomotion behaviours, the direction (or sign) of the 'Diff_Deep' value was used by both algorithms, indicating the direction of movement and demonstrating the value of non-accelerometer sensors in helping differentiate behaviours, while negative or positive values of StX gave information about the inclination of the body (upward-facing or downward-facing). Dynamic acceleration was particularly useful in the hawksbill and green turtle CART model to help discriminate 'interaction' and 'SH hori'. The interactions between the two adult turtles were brief and fast, leading to high values for dynamic acceleration as one of the turtles attacked or escaped (Fig. 2).

In our attempt to create a shared ethogram, we described as much behavioural detail as possible in order to make models most applicable to free-living turtles. However, as the three turtles expressed the behaviours with different frequencies, we were obliged to build two distinct models, both of which sought to conserve the observed behavioural characteristics (body posture, activity, direction, etc.) as closely as possible. This difference in the expression of behaviours might be primarily due to the size/age difference between the animals, the juvenile loggerhead being half the size of the other two (adult) species. In addition, turtle buoyancy also determines dynamic acceleration signals (Yasuda and Arai, 2009; Fossette et al., 2010) and this may have led to different behavioural expressions between the juvenile and the adults. The

loggerhead turtle models notably gave a global accuracy that was about 10 points lower than the adult models due to a higher number of behaviours, and this concurs with other studies that have shown a similar decrease of CART accuracy with the addition of behaviours (Shamoun-Baranes et al., 2012; Nishizawa et al., 2013). Again, as we obtained data from only one loggerhead individual, our sample size prohibits proper consideration of this. Our first CART model building tests showed clearly, however, that an increase of the available segment number (110) in both algorithms led to a rapid decline in the precision and recall indices of poorly represented behaviours. Thus, this model currently does not seem particularly compelling for use on free-living individuals and should be consolidated with extra data.

Limits of using captive animals

As with other wild animal species (Hogan et al., 1988; Birke, 2002; Montaudouin and Le Pape, 2004), captivity is expected to profoundly affect the extent and type of behaviours exhibited by sea turtles by virtue of the restricted space and poorly enriched environment. However, the environment for the turtles of Aquarium La Rochelle is conceived to encourage them to conserve their natural behaviours, such as resting in various hiding places within their aquarium and searching for food in the water column and on the bottom. For this reason, the food-searching behaviour 'grazing' was identified in both the adult and juvenile models while 'prey' was discriminated only in the loggerhead turtle model. It was, however, problematic that there was a very low incidence of such behaviour in our study. Nonetheless, the success of identification of 'prey' and 'grazing' behaviours indicates that tags such as ours deployed on free-living animals could point towards food ingestion events, an important part of turtle ecology.

An obvious limitation of our system was manifest in our models being unable to discriminate passive movements (notably gliding up and/or down the water column), behaviours that have been noted from free-living turtles (Yasuda and Arai, 2009; Fossette et al., 2010). This was because these phases are highly transitory in captivity and, anyway, particular pressure conditions (associated with depth) are necessary for the overall turtle body density to differ enough from that of seawater for these to take place. For example, Yasuda and Arai (2009) estimated that wild green turtles can glide down passively at depths of between 12 and 20 m. Our 4 m deep tanks were, therefore, inadequate in this respect.

Of particular note is that the decision trees obtained from the CART algorithm, as well as the importance of variables indicated by the Random Forest algorithm, showed that dynamic acceleration values were used little to discriminate behaviours, with models being primarily reliant on posture and pressure differences. This contrasts with results obtained from accelerometers deployed on free-living turtles, where dynamic acceleration values figure extensively in activity budget quantification and in discussing the energy management strategies of these animals (Hochscheid et al., 1999; Lagarde et al., 2008; Fossette et al., 2012). In fact, dynamic acceleration did not vary significantly between sea turtle behaviours in our study, which we assume was a consequence of the constraints of captivity. This is not just related to the limited space per se but also reflects the amount of 'effort' invested in any movement by captive animals compared with their wild counterparts (Shepherdson et al., 1993; Veasey et al., 1996). Interestingly, in the CART models, 'interaction' and 'prey', were among the few behaviours discriminated by dynamic acceleration, both of which are expected in wild animals and elicited some vigour in the captive animals, for obvious reasons.

Sea turtle flipper beating during travelling produces a clear, regular waveform in the heave axis (Shepard et al., 2008), a pattern that is also characteristic in swimming penguins and flying birds (Watanabe et al., 2005; Lagarde et al., 2008; Shamoun-Baranes et al., 2012; Nishizawa et al., 2013). Given the low flipper beat frequency of turtles (Yasuda and Arai, 2009) and the limited dimensions of our study tanks, it proved challenging to obtain clear flipper-beat signals of our turtles during swimming (noting that a temporal window of >6 s and >4 s is needed for 2 flipper beats for the adult and juvenile animals, respectively), which also correspondingly reduced the number of segments used to build the models.

Perspectives and conclusions

The development of remote sensors, such as 3D accelerometers, allows us to acquire new information about the behavioural ecology of enigmatic species in the wild. This is particularly germane for threatened species. For this reason, studies seeking to validate sensor signals for turtle behaviours are important in helping conservation efforts (Sutherland, 1998). This study is the first to validate accelerometer data to identify the behaviours of turtles in water. For this, we suggest using two supervised algorithms in order to combine the advantages of both. While the Random Forest algorithm is a powerful classification algorithm, upstream use of the CART algorithm highlighted 'confused' behaviours and allowed us to refine our analysis in order to build the most accurate Random Forest model. Despite the obvious limitations of studies on captive animals, our work indicates that this approach is a promising first step in helping to identify the suite of behaviours exhibited by sea turtles. We hope that this study will help catalyse the next stage in the process, which is to have the derived models tested on other watchable captive sea turtle species, with a view to taking the system into the wild. Ultimately, the aspiration is to use this approach to provide data that will improve management plans for these endangered species.

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Competing interests

The authors declare no competing or financial interests.

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Supplementary information

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References

- Bao, L. and Intille, S. S. (2004). Activity recognition from user-annotated acceleration data. In *Pervasive Computing* (ed. A. Ferscha and F. Mattern). Pervasive 2004. Lecture Notes in Computer Science, vol. 3001. Berlin: Springer.
- Baudouin, M., de Thoisy, B., Chambault, P., Berzins, R., Entraygues, M., Kelle, L., Turny, A., Le Maho, Y. and Chevallier, D. (2015). Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*). *Biol. Conserv.* **184**, 36–41.
- Birke, L. (2002). Effects of browse, human visitors and noise on the behavior of captive orangutans. *Anim. Welf.* **11**, 189–202.
- Breiman, L. (2001). Random forests. *Mach. Learn.* **45**, 5–32.
- Breiman, L., Friedman, J., Stone, C. J. and Olshen, R. (1984). *Classification and Regression Trees*. Berlin: Springer (Wadsworth and Brooks).
- Brown, D. D., Kays, R., Wikelski, M., Wilson, R. and Klimley, A. P. (2013). Observing the unwatchable through acceleration logging of animal behavior. *Anim. Biotelemetry* **1**, 20.
- Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2157–2162.
- Casale, P., Pujol, O. and Radeva, P. (2011). Human activity recognition from accelerometer data using a wearable device. *Pattern Recognit. Image Anal.* **6669**, 289–296.
- Chambault, P., Pinaud, D., Vantrepotte, V., Kelle, L., Entraygues, M., Guinet, C., Berzins, R., Bilo, K., Gaspar, P., de Thoisy, B. et al. (2015). Dispersal and diving adjustments of the green turtle *Chelonia mydas* in response to dynamic environmental conditions during post-nesting migration. *PLoS ONE* **10**, e0137340.
- Chambault, P., Roquet, F., Benhamou, S., Baudena, A., Pauthenet, E., de Thoisy, B., Bonola, M., Dos Reis, V., Crasson, R., Brucker, M. et al. (2017). The Gulf Stream frontal system: a key oceanographic feature in the habitat selection of the leatherback turtle? *Deep Res. Part I Oceanogr. Res. Pap.* **123**, 35–47.
- Chevallier, D., Handrich, Y., Georges, J.-Y., Baillon, F., Brossault, P., Auroret, A., Le Maho, Y., Massemin, S. (2010). Influence of weather conditions on the flight of migrating black storks. *Proc. R. Soc. B Biol. Sci.* **277**:2755–2764.
- Collins, P. M., Green, J. A., Warwick-Evans, V., Dodd, S., Shaw, P. J. A., Arnould, J. P. Y. and Halsey, L. G. (2015). Interpreting behaviors from accelerometry: a method combining simplicity and objectivity. *Ecol. Evol.*
- Dodge, K. L., Galuardi, B., Miller, T. J. and Lutcavage, M. E. (2014). Leatherback turtle movements, dive behavior, and habitat characteristics in ecoregions of the Northwest Atlantic Ocean. *PLoS ONE* **9**, e91726.
- Ellis, K., Godbole, S., Marshall, S., Lanckriet, G., Staudenmayer, J. and Kerr, J. (2014). Identifying active travel behaviors in challenging environments using GPS, accelerometers, and machine learning algorithms. *Front. Public Heal.* **2**, 36.
- Enstipp, M. R., Ciccione, S., Gineste, B., Milbergue, M., Ballorain, K., Ropert-Coudert, Y., Kato, A., Plot, V. and Georges, J.-Y. (2011). Energy expenditure of freely swimming adult green turtles (*Chelonia mydas*) and its link with body acceleration. *J. Exp. Biol.* **214**, 4010–4020.
- Fehlmann, G., O'Riain, M. J., Hopkins, P. W., O'Sullivan, J., Holton, M. D., Shepard, E. L. C. and King, A. J. (2017). Identification of behaviours from accelerometer data in a wild social primate. *Anim. Biotelemetry* **5**, 6.
- Forin-Wiart, M.-A., Poulle, M. L., Hubert, P., Chevallier, D., Georges, J. and Handrich, Y. (2014). Use of tri-axial accelerometers: towards the identification of when and how often cats hunt? The 5th International Bio-logging Science Symposium. Strasbourg, France.
- Fossette, S., Gleiss, A. C., Myers, A. E., Garner, S., Liebsch, N., Whitney, N. M., Hays, G. C., Wilson, R. P. and Lutcavage, M. E. (2010). Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle. *J. Exp. Biol.* **213**, 4074–4083.
- Fossette, S., Schofield, G., Lilley, M. K. S., Gleiss, A. C. and Hays, G. C. (2012). Acceleration data reveal the energy management strategy of a marine ectotherm during reproduction. *Funct. Ecol.* **26**, 324–333.
- Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.* **2**, 23–33.
- Graf, P. M., Wilson, R. P., Qasem, L., Hackländer, K. and Rosell, F. (2015). The use of acceleration to code for animal behaviours; a case study in free-ranging Eurasian beavers *Castor fiber*. *PLoS ONE* **10**, e0136751.
- Halsey, L. G., Jones, T. T., Jones, D. R., Liebsch, N. and Booth, D. T. (2011). Measuring energy expenditure in sub-adult and hatchling sea turtles via accelerometry (Y Ropert-Coudert, Ed.). *PLoS ONE* **6**, e22311.

- Hart, K. M. and Hyrenbach, K. D. (2010). Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endanger. Species Res.* **10**, 9-20.
- Hochscheid, S., Godley, B. J., Broderick, A. C. and Wilson, R. P. (1999). Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* **185**, 101-112.
- Hogan, E. S., Houpt, K. A. and Sweeney, K. (1988). The effect of enclosure size on social interactions and daily activity patterns of the captive Asiatic wild horse (*Equus przewalskii*). *Appl. Anim. Behav. Sci.* **21**, 147-168.
- Hubel, T. Y., Myatt, J. P., Jordan, N. R., Dewhirst, O. P., McNutt, J. W. and Wilson, A. M. (2016). Additive opportunistic capture explains group hunting benefits in African wild dogs. *Nat. Commun.* **7**, 11033.
- Iucnredlist.org. (2018). The IUCN Red List of Threatened Species. [online] Available at: <http://www.iucnredlist.org/> [Accessed 12 Jan 2018].
- Jack, K. M., Lenz, B. B., Healan, E., Rudman, S., Schoof, V. A. M. and Fedigan, L. (2008). The effects of observer presence on the behavior of *Cebus capucinus* in Costa Rica. *Am. J. Primatol.* **70**, 490-494.
- Kooyman, G. L. (2003). Genesis and evolution of bio-logging devices: 1963–2002. *Mem. Natl. Polar Res. Inst.* **5**, 15-22.
- Ladds, M. A., Thompson, A. P., Kadar, J.-P., Slip, D., Hocking, D. and Harcourt, R. (2017). Super machine learning: improving accuracy and reducing variance of behaviour classification from accelerometry. *Anim. Biotelemetry* **5**, 8.
- Lagarde, F., Guillon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., Slimani, T. and El Mouden, E. H. (2008). Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Anim. Behav.* **75**, 319-329.
- Montaudouin, S. and Le Pape G. (2004). Comparison of the behaviour of European brown bears (*Ursus arctos arctos*) in six different parks, with particular attention to stereotypies. *Behav. Processes* **67**, 235-244.
- Narazaki, T., Sato, K., Abernathy, K. J., Marshall, G. J. and Miyazaki, N. (2009). Sea turtles compensate deflection of heading at the sea surface during directional travel. *J. Exp. Biol.* **212**, 4019-4026.
- Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J. Exp. Biol.* **215**, 986-996.
- Nishizawa, H., Noda, T., Yasuda, T., Okuyama, J., Arai, N. and Kobayashi, M. (2013). Decision tree classification of behaviors in the nesting process of green turtles (*Chelonia mydas*) from tri-axial acceleration data. *J. Ethol.* **31**, 315-322.
- Okuyama, J., Kawabata, Y., Naito, Y., Arai, N. and Kobayashi, M. (2009). Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles. *Endanger. Species Res.* **10**, 39-45.
- Powers, D. M. W. (2007). Evaluation: from precision, recall and F-factor to ROC, informedness, markedness and correlation. *Int. J. Mach. Learn. Tech.* **2**, 37-63.
- Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE* **7**, e31187.
- Resheff, Y. S., Rotics, S., Harel, R., Spiegel, O. and Nathan, R. (2014). AcceleRater: a web application for supervised learning of behavioral modes from acceleration measurements. *Mov. Ecol.* **2**, 27.
- Schneirla, T. C. (1950). The relationship between observation and experimentation in the field study of behavior. *Ann. N. Y. Acad. Sci.* **51**, 1022-1044.
- Shamoun-Baranes, J., Bom, R., van Loon, E. E., Ens, B. J., Oosterbeek, K. and Bouten, W. (2012). From sensor data to animal behaviour: an oystercatcher example (GG de Polavieja, Ed.). *PLoS ONE* **7**, e37997.
- Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A., Morgan, D. T., Myers, A. E. et al. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endanger. Species Res.* **10**, 47-60.
- Shepherdson, D. J., Carlstead, K., Mellen, J. D. and Seidensticker, J. (1993). The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biol.* **12**, 203-216.
- Soltis, J., Wilson, R. P., Douglas-Hamilton, I., Vollrath, F., King, L. E. and Savage, A. (2012). Accelerometers in collars identify behavioral states in captive African elephants *Loxodonta africana*. *Endanger. Species Res.* **18**, 255-263.
- Soltis, J., King, L., Vollrath, F. and Douglas-Hamilton, I. (2016). Accelerometers and simple algorithms identify activity budgets and body orientation in African elephants *Loxodonta africana*. *Endang. Species Res.* **31**, 1-12.
- Spotila, J. R. (2004). *Sea Turtles: A Complete Guide to their Biology, Behavior, and Conservation*. Baltimore, MA: The John Hopkins University Press.
- Sutherland, W. J. (1998). The importance of behavioural studies in conservation biology. *Anim. Behav.* **56**, 801-809.
- Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. and Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 2163-2176.
- Veasey, J. S., Waran, N. K. and Young, R. J. (1996). On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. *Animal Welfare* **5**, 139-153.
- Walker, J. S., Jones, M. W., Laramee, R. S., Holton, M. D., Shepard, E. L. C., Williams, H. J., Scantlebury, D. M., Marks, N. J., Magowan, E. A., Maguire, I. E. et al. (2015). Prying into the intimate secrets of animal lives: software beyond hardware for comprehensive annotation in 'Daily Diary' tags. *Mov. Ecol.* **3**, 1-16.
- Watanabe, Y., Baranov, E. A., Sato, K., Naito, Y. and Miyazaki, N. (2004). Foraging tactics of Baikal seals differ between day and night. *Mar. Ecol. Prog. Ser.* **279**, 283-289.
- Watanabe, S., Izawa, M., Kato, A., Ropert-Coudert, Y. and Naito, Y. (2005). A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *Appl. Anim. Behav. Sci.* **94**, 117-131.
- Watanabe, S., Sato, K., Ponganis, P. J., Groscolas, R. and Ponganis, P. (2012). Activity time budget during foraging trips of emperor penguins (A Chiaradia, Ed.). *PLoS ONE* **7**, e50357.
- Willener, A. S. T., Handrich, Y., Halsey, L. G. and Strike, S. (2015). Effect of walking speed on the gait of king penguins: an accelerometric approach. *J. Theor. Biol.* **387**, 166-173.
- Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081-1090.
- Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endanger. Species Res.* **4**, 123-137.
- Yasuda, T. and Arai, N. (2009). Changes in flipper beat frequency, body angle and swimming speed of female green turtles *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* **386**, 275-286.
- Yoda, K., Sato, K., Niizuma, Y., Kurita, M. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adélie penguins. *J. Exp. Biol.* **3126**, 3121-3126.