Fine-scale body and head movements allow to determine prey capture events in the Magellanic Penguin (Spheniscus magellanicus)

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ORIGINAL PAPER

Fine-scale body and head movements allow to determine prey capture events in the Magellanic Penguin (*Spheniscus magellanicus*)

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Abstract
The identification of when, how and where animals feed is essential to estimate the amount of energy they obtain and to study the processes associated with prey search and consumption. We combined the use of animal-borne video cameras and accelerometers to characterise the body and head movements associated to four types of prey capture behaviours in the Magellanic Penguin (*Spheniscus magellanicus*). In addition, we evaluated how the K-Nearest Neighbour (K-NN) algorithm recognized these behaviours from acceleration data. Finally, we compared the total capture and the capture per unit time (CPUT) derived by identifying prey capture events using the K-NN algorithm to that derived by counting undulations in the dive profile ("wiggles"). During captures, body and head movements were highly variable in the tridimensional space. Energy expenditure (i.e., VeDBA values) during diving periods with prey captures was from three to four times higher than during controls diving periods (i.e., with no capture events). The K-NN classification resulted effective and showed accuracy scores above 90% when considering both head and body related features. In addition, when captures were estimated using the K-NN method, the CPUT was similar or higher to that estimated by counting wiggles. Our study contributes to the knowledge of the trophic ecology of this species and provides an alternative method for estimating prey consumption in the Magellanic Penguin and other diving seabirds.

Introduction

The identification of when, how and where animals feed is essential to estimate the amount of energy they obtain (Sala et al. 2012a, b; Gallon et al. 2013; Skinner et al. 2014), to study the processes associated with prey search and consumption (Watanabe et al. 2019), and to evaluate population responses to environmental changes (Carroll et al. 2018). In the marine realm, prey capture events by top predators have been particularly difficult to detect, since animals feed far away from the coast and, in most of the cases, below the water surface (but see Takahashi et al. 2004b; Redfern et al. 2006; Naito 2007). Fortunately, these limitations have been tackled by the employment of sensors that provide indirect parameters of prey capture events such as stomach, oesophageal or visceral temperature (Wilson et al. 1992; Charrassin et al. 2001; Austin et al. 2006), beak or mouth opening (Wilson et al. 2002a, b; Takahashi et al. 2004a; Fossette et al. 2008), or head and jaw movements (Ropert-Coudert et al. 2004; Liebsch et al. 2007; Okuyama et al. 2013; Guinet et al. 2014).

During the last three decades the indirect detection of capture events by means of electronic signals has been complemented by the deployment of video or still images loggers (Ponganis et al. 2000; Heithaus et al. 2002). Due to their size and weight, the first cameras were deployed on large species such as the Loggerhead (*Caretta caretta*) and Leatherback (*Dermochelys coriacea*) turtles (Marshall 1998), the Weddell Seal (*Leptonychotes weddellii*) (Davis et al. 1999) and the Emperor Penguin (*Aptenodytes forsteri*) (Ponganis et al. 2000). However, technological advances enabled the development of small video recorders that can even be deployed on species of the size of a crow (Rutz and Troscianko 2013). Even though, due to battery limitations, small video cameras cannot record for long periods of time, the information they provide is particularly valuable to validate electronic signals recorded by other sensors such as tri-axial accelerometers (Watanabe and Takahashi 2013; Carroll et al. 2014; Viviant et al. 2014; Volpov et al. 2015). Contrary to cameras, accelerometers can record at high frequencies (e.g., 300 Hz or higher) and for longer periods of time (e.g., up to 60 days at 25 Hz for a 3 g device). Once the acceleration signal associated to a particular behaviour (e.g., capture event) has been validated, the behaviour can be identified from acceleration signals without the need of a camera. Using video-cameras in the wild to determine prey capture event signals has a great potential and during the last years has allowed researchers to test Optimal Foraging Theory predictions in the wild (Watanabe et al. 2014; Foo et al. 2016; Chimienti et al. 2017), to determine the distribution of prey encounter events in relation to oceanographic features such as water temperature, salinity and light level (Guinet et al. 2014), and to examine relationships between prey distribution and spatially explicit patterns of prey capture (Carroll et al. 2017). Moreover, since dynamic acceleration can predict the costs of movement for terrestrial, aquatic and even aerial locomotion (by means of overall dynamic body acceleration (ODBA) or vectorial dynamic body acceleration (VeDBA), see Halsey et al. 2011; Qasem et al. 2012; Wilson et al. 2019), it offers the opportunity to estimate the energy expenditure associated to both pursuit and capture behaviours (Wilson et al. 2013; Tennessen et al. 2019).

Identification of discrete animal behaviours by means of acceleration data is a tedious and time consuming task, especially for big data. This led researchers to consider machine learning algorithms to automatically classify large acceleration datasets into behavioural classes (Nathan et al. 2012; Ladds et al. 2017; Valletta et al. 2017; Jeantet et al. 2018; Bidder et al. 2020; Chakravarty et al. 2020). Among the supervised learning algorithms commonly used are the K-Nearest Neighbour (K-NN) algorithm (Bidder et al. 2014), Supported Vector Machines (SVMs) (Cortes and Vapnik 1995; Martiskainen et al. 2009), Classification and Regression Trees (CART), Random Forests (RFs) (Breiman

2001; Hutchinson and Gigerenzer 2005; Cutler et al. 2007; Nadimi et al. 2008; Pavey et al. 2017) and Artificial Neural Networks (ANNs) (Nathan et al. 2012; Nadimi et al. 2012; Gutierrez-Galan et al. 2018). These algorithms have recognized different behaviours such as flying, walking and swimming, with a high rate of accuracy (Grünewälder et al. 2012; McClune et al. 2014; Resheff et al. 2014; Williams et al. 2015; Sur et al. 2017; Bidder et al. 2020). In the marine environment, feeding events have been detected by means of SVMs and CART algorithms with accuracies that range between 78 and almost 90% in Little penguins (*Eudyptula minor*), Australian sea lions (*Neophoca cinerea*), seals (*Arctocephalus pusillus doriferus*, *A. forsteri*, *A. tropicalis*) and sea turtles (*Chelonia mydas, Eretmochelys imbricata* and *Caretta caretta*) (Carroll et al. 2014; Ladds et al. 2017; Jeantet et al. 2018).

The Magellanic Penguin (*Spheniscus magellanicus*) is the most abundant seabird species breeding along the Patagonian coast of Argentina, being widely distributed from Islote Lobos, Río Negro Province (41°S) to the Beagle Channel, Tierra del Fuego (54°S) (Yorio et al. 1999; Schiavini et al. 2005; Pozzi et al. 2015). Magellanic penguins are visual hunters (Handley et al. 2018) that feed mainly on pelagic schooling fish such as Argentinean Anchovy (*Engraulis anchoita*) and Patagonian Sprat (*Sprattus fuegensis*) north of 44°S and south of 50°S, respectively (Frere et al. 1996). Schools are usually approached from below and depolarized making prey more susceptible to predation (Ropert-Coudert et al. 2001; Simeone and Wilson 2003; Handley et al. 2018). Traditionally, Magellanic Penguin prey consumption has been estimated by the quantification of beak opening events (Wilson et al. 2002a, b; Takahashi et al. 2004a) and by means of stomach or esophagus temperature sensors (Wilson et al. 1992; Charrassin et al. 2001). Even though these methods proved to be highly accurate (Hanuise et al. 2010), they are quite invasive, complex to implement and fail to detect multiple rapid ingestions of small prey (Viviant et al. 2010; Kokubun et al. 2011). A less accurate but simpler alternative for the estimation of prey capture events is to detect and quantify undulations in the bottom phase dive profile commonly known as "wiggles" (Wilson and Liebsch. 2003; Bost et al. 2007; Sala et al. 2012b). However, one drawback the wiggles technique presents is that undulations are computed exclusively during the bottom phase of dives and, even though most of the captures take place during this diving phase, Magellanic penguins (as do other penguin species), also capture prey in other diving phases such as during the ascent and close to the water surface on dives less than 2 m depth (Gómez-Laich et al. 2018).

In the present paper, we first describe the body and head acceleration signals associated to four different types of Magellanic penguins' prey capture events: (1) those taking place at the bottom phase of dives, (2) those taking place

during the ascent phase, (3) those occurring during the first meters of the water column when birds are resurfacing, and (4) those inside a shoal independently of the diving phase in which they occurred. Secondly, due to its computationally simplicity and usefulness in classifying different types of behaviours (Keller et al. 1985; Bidder et al 2014, 2020) we investigated if the K-NN algorithm can identify these four types of feeding behaviours from body and head acceleration data. Finally, we compared the amount of captures and capture per unit time (CPUT) derived by identifying prey capture events using the K-NN algorithm to that derived by counting the number of undulations in the dive profile (i.e., wiggles) of individuals from two patagonian colonies that exhibit different foraging dynamics, namely Punta Norte/San Lorenzo and Cabo dos Bahías.

Materials and methods

Study site

Fieldwork was conducted at Punta Norte/San Lorenzo (42°04'S, 63°49'W) and Cabo dos Bahías (44°54'S, 65°32'W) Magellanic Penguin colonies during the early chick-rearing period between November the 25th and December the 10th of 2015 and 2016.

Deployment of devices

Nine Magellanic penguins (five from Punta Norte/San Lorenzo and four from Cabo dos Bahías) brooding at least one chick less than 10 days, were instrumented with: (1) a submersible video camera (DVL400M065, Little Leonardo Corporation, Japan, 61 mm in length, 21 mm in width, 15 mm in height, 29 g, 1,280×960 pixels, 30 frames per second, 6 h battery life), (2) an electronic activity recorder with pressure, temperature and tri-axial acceleration sensors (AXY Depth, Technosmart, Rome, Italy, 31 mm in length, 12 mm in width, 11 mm in height, 6.5 g), and 3) an accelerometer (Technosmart, Rome, Italy, 50 mm in length, 8 mm in width, 3 mm in height, 2 g). Ten additional Magellanic penguins (five from Punta Norte/San Lorenzo and five from Cabo dos Bahías) were equipped with AXY Depth only. Cameras were programmed to record continuously, five started recording in the morning of the day after deployment, since Magellanic penguins begin foraging at dawn (Sala 2013) and the remaining four started recording on the day after deployment (12 pm approximately). The electronic activity recorders (i.e., AXY Depth) were set to record acceleration at 25 Hz and pressure and temperature at 1 Hz, while the accelerometers were programmed to record at 25 Hz.

Each bird was captured of its nest and equipped with the accelerometer on the head, the camera on the upper back
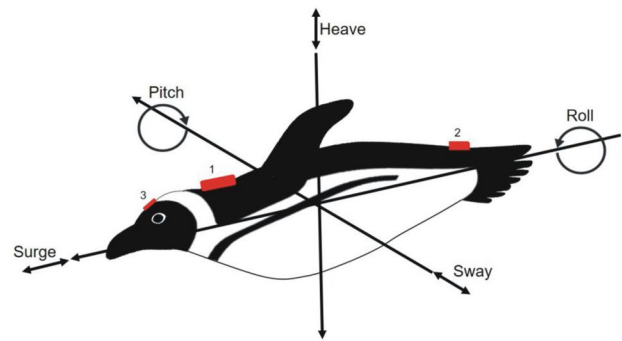

Fig. 1 Ilustration showing how the surge, sway and heave acceleration measurements relate to the penguin's movements and how the pitch and roll values relate to the bird's body angle. The position of (1) the camera logger, (2) the AXY Depth, and (3) the head accelerometer is also indicated

and the AXY Depth on the lower back (Fig. 1). The three instruments were attached to the feathers using Tesa® tape following Wilson et al. (1997). In all cases, the instrumentation procedure was completed in less than five minutes and birds immediately returned to the nest. Each penguin was allowed to forage for a single trip before the devices were retrieved. All birds carrying devices continued to feed their chicks normally after being instrumented. At Cabo dos Bahías trips from instrumented animals were similar in duration to those from uninstrumented animals (G. Blanco and F. Quintana unpub. data). Unfortunately, at Punta Norte we did not document the trip duration of unequipped birds. However, during both years (2015 and 2016) instrumented animals from this colony foraged for about 24 h. This is the average foraging trip duration for "normal" years and under this type of years the harmful effects of external tags would be practically negligible (Wilson et al. 2015).

Data analysis

Fifty hours of video recording were analysed using the Kinovea free video player software (Kinovea Creative Commons Attribution 2006). On the video images, dives and dive phases (i.e., descent, bottom and ascent) were visually distinguished by looking at penguins' body position in relation to light intensity. The descent phase was defined as the interval from the time the camera was being observed to submerge to the time the animal was observed to stop swimming downwards. The ascent phase was defined as the interval from the time the animal was observed to swim upwards until the bird reached the sea surface. The bottom phase was defined as the interval from the time the bird finished swimming downwards until it started swimming upwards. Four types of prey capture events were identified from the videos: (1) isolated prey capture events taking place

during the bottom phase of dives performed at depths where visual inspection was possible (i.e., a maximum of 40 m depth), (2) isolated prey capture events occurring during the ascent phase, (3) isolated prey capture events taking place during the first meters of the water column during shallow dives (i.e., < 6 m) when penguins were resurfacing, and (4) prey capture events inside fish shoals observed at depths that varied between 3 and 40 m, independently of the diving phase in which they occurred (Fig. 2). To compare movements associated to captures to those associated to regular swimming, for each prey capture behaviour an equal number of swimming sections in which no prey capture or capture attempt took place were randomly selected. These selected swimming periods were similar in depth and duration to capture events and were considered as "control" sections.

The time stamps of depth, body and head acceleration data were aligned visually to within ± 0.5 s using the Software Multi-trace (Jensen Software Systems, Laboe,

Germany). After this, the behaviours identified in the videos were matched to the acceleration and depth data using custom matching functions in R version 3.6.1 (R Core Team 2019) based on a common time vector synced to both datasets. The acceleration signal associated to each capture extended from the moment a change in the regular acceleration profile was detected to the moment the acceleration signal regularized. That selection was made because the reaction associated with a feeding stimulus also includes the instant before and after the capture takes place. Once identified, we determined the total acceleration of translational motions: surge (horizontal in the direction of the movement), sway (side to side) and heave (vertical) (Fig. 1) from each recognized behaviour and its respective control period. The static and dynamic acceleration component of each axis was obtained using a running mean of 3 s following Shepard et al. (2008). The static component of each channel was used to compute

Fig. 2 Still frames obtained from a video logger attached to the back of a Magellanic Penguin (*Spheniscus magellanicus*). Image **a** shows a penguin pursuing a fish during the bottom phase of a dive, **b** a penguin pursuing a fish during the ascent phase of a dive, **c** a penguin capturing fish close to the sea surface and **d** a penguin pursuing fish through a shoal

the pitch and roll angles (i.e., rotational motion) (Fig. 1) and smoothed over 1 s (Gunner et al. 2020). VeDBA was calculated using the vectorial sum of the dynamic components of acceleration from the three axes (Qasem et al. 2012) and smoothed over 1 s to eliminate individual strides and have a better estimation of the costs of movement (Wilson et al. 2019).

To characterise penguins' movements, once the tri-axial acceleration signals (from the body and the head) of captures and controls were identified, we calculated the following parameters from the raw information of each acceleration channel: mean, standard deviation, minimum and maximum. Furthermore, the same parameters mentioned above were computed for body pitch angle, body roll angle, body VeDBA and depth.

K-Nearest Neighbour analysis

For the automatic classification analysis we implemented the K-Nearest Neighbour (K-NN) algorithm with Euclidean distance to identify each of the eight types of behaviours (i.e., the four prey capture behaviours previously defined above and the four controls for such behaviours). The following features were calculated for each of the six raw acceleration channels (three from the body and three from the head), VeDBA, body pitch and roll angles and depth: mean, minimum, maximum and standard deviation. All these features were calculated using a sliding sample window of 2 s (equaling 50 samples of data) with a 1.96 s overlap (49 samples of data). Since the distance formula employed in the K-NN method is highly dependent on the scale in which variables are measured (Lantz 2015), features were rescaled using the min–max normalization.

Due to the fact that we had an imbalanced data set, with some categories less represented than others, we balanced the full sample by randomly selecting similar proportions of each type of prey capture behaviour. After this, we randomly divided the segmented and annotated data into a training data set (70% of the data) and a testing data set (30% of the data). The training data set was used to train the model by performing 10 repetitions of 10-fold cross-validation by means of the *train* function from the *caret* R package (Kuhn 2016) using a *tuneLength* parameter value of 20. Once the model had been trained and the optimal K value estimated, we used the *predict* function to classify the testing data set. The *confusionMatrix* function allowed us to compare the predicted classes of our testing data set with the known classes (determined by the videos) and to determine for each class in the data set if the classification was either True Positive (TP), False Positive (FP), True Negative (TN) or False Negative (FP). After this, the following series of performance metrics were calculated:

$$Sensitivity = \frac{TP}{TP + FN}$$

$$Specificity = \frac{TN}{TN + FP}$$

$$Prevalence = \frac{TP + FN}{TN + TP + FN + FP}$$

$$Accuracy = \frac{TN + TP}{TN + TP + FN + FP}$$

$$Positive\ predicted\ value = \frac{TP}{TP + FP}$$

$$Negative\ predicted\ value = \frac{TN}{TN + FN}$$

To determine if the classification performance diminished when only the body or the head features were taken into account, the above mentioned procedure was ran two more times: (1) considering only the body features and (2) considering only the head features.

Prey capture rates

The diving behaviour of 10 additional Magellanic penguins (five from Punta Norte/San Lorenzo and five from Cabo dos Bahías) (see above), carrying only an AXY Depth on the lower back, was analysed using the program MTDIVE (Jensen Software System) (see Sala et al. 2012b, 2014 for details). For each submersion that exceeded 2 m depth, a single wiggle or undulation in the dive profile (Simeone and Wilson 2003) was defined as two or three serial points of inflexion (SPI) of > 0.5 m/s (see Sala et al. 2012b for details). Each wiggle was taken to represent a prey capture event and was used to derive the capture per minute of time underwater (CPUT). In addition, the best K-NN algorithm using only body acceleration and depth derived features (see results) was applied to the foraging trip data of these 10 penguins. Data were first preprocessed to obtain all the previously defined features over 2 s segments with a 1.96 s overlap. After running the K-NN, for each dive identified by the MTDIVE (see above), we determined the CPUT. To do this, first we summed the amount of time assigned to each type of capture. To translate the amount of time invested on each capture to the number of consumed prey items, based on the video information, a capture at the bottom of a dive was considered to have a mean duration of 19 s, a capture during the ascent phase 20 s, a capture inside a shoal 23 s and a capture near the surface 7 s. Finally, the number of each type of capture per dive was summed and used to calculate the CPUT.

Statistical analysis

The acceleration parameters (mean, standard deviation, minimum and maximum), pitch, roll, body VeDBA and depth of each type of prey capture event and its corresponding control were compared through t or Mann–Whitney test depending on data characteristics. For each of these analyses, data normality was tested through the Shapiro–Wilk test and homoscedasticity by means of F-test.

Differences between the mean CPUT estimated using the K-NN algorithm and wiggles for each animal were compared by a Linear Mixed Model (LMM) using the *glmmTMB* function (Brooks et al. 2017). In this test, CPUT was set as the response variable, method (K-NN vs wiggles) was set as a fixed explanatory variable, while dive was set as a random explanatory variable. The significance of the fixed factor was tested by comparing the model with and without it using the function *anova* of the *stats* package for R 3.6.1 (R Core Team 2019). All values are reported as means ± s.d. and all differences were considered significant at $p < 0.05$.

Results

Prey capture behaviour

During the recorded period (50 h), a total of 65 prey capture events and an equal number of control behaviours were identified. Of the total capture events, 20 (30.8%) took place during the bottom phase, 15 (23.1%) during the ascent phase (an example of this is given in Electronic Supplementary Material ESM 1), eight (12.3%) on the first meters of the water column and 22 (33.8%) inside of a fish shoal. Among all capture events, those that took place during the first meters of the water column were the least frequent and occurred at a mean depth of 6 m ± 5.5 m. Captures inside fish shoals were not associated to any dive phase; in some cases they took place along all the dive phases (descent, bottom and ascent), while in others, they occurred in one or two of them.

Body acceleration and VeDBA

During the four types of prey capture events, Magellanic Penguin body movements were highly variable in the tridimensional space (indicated by higher standard deviation values) in comparison to control periods (Table 1). All capture events except those that took place during the first meters of the water column presented a higher variation in pitch and roll angles than those registered during controls (Table 1). Only during captures at the bottom and inside of a shoal, the dorso-ventral (heave) mean acceleration values were smaller than during controls (Table 1).

While swimming and capturing prey along the bottom phase of dives, penguins slightly tilted their body up (swimming mean pitch angle = 15.72° ± 10°, capture at the bottom mean pitch angle = 22.90° ± 14°) (Table 1). Penguins ascended passively along the water column, without any variation in the tri-axial body acceleration values and with a mean pitch body angle of 45° ± 17° (Table 1). During captures at the bottom and during the ascent animals made substantial movements along the three axes (Fig. 3a, b).

During the four different types of prey capture events mean VeDBA values were similar (ANOVA, $F_{3,61} = 1.39$, $p = 0.25$) and oscillated around 0.5, reaching values up to 2.5 during captures inside a shoal and close to the water surface (Fig. 4). Mean VeDBA values during capture events were between three and four times greater than the mean VeDBA values of control behaviours (Table 1).

Head acceleration

Similarly to body movements, during prey captures, head movements presented an important variation in the three dimensions in comparison to control behaviours (Table 2). Mean acceleration values were similar between captures and controls for all head motion axes, except for the translation of the head in the vertical axis (heave). The mean vertical motion of penguin head during captures at the bottom, near the surface and inside a shoal were lower than controls (Table 2). During captures at the bottom, head dorso-ventral movements presented a cyclic pattern with values fluctuating around 1 g (Fig. 3c). In contrast, sway and surge acceleration values did not present great oscillations (Fig. 3c). During the ascent, head movements showed a regular pattern without much variation in none of the three axes (Fig. 3d). However, captures were characterised by high fluctuations in the acceleration signals along the three axes (Fig. 3d).

K-NN classifier

A total of 8783 behavioural segments were used for the K-NN, 6148 segments were used for training (70%) and 2632 for testing (30%). The three K-NN models performed best with a K value of 5 (Fig. 5) and presented balanced accuracy values above 85%, meaning that more than 85% of the segments were correctly classified. The K-NN including all the features showed the highest classification accuracy (93.6% overall accuracy, Kappa = 0.93), followed by the K-NN including the body and depth features with classification of every class > 89% (91.3% overall accuracy, Kappa = 0.90) (Table 3). The less accurate K-NN model was the one that only included the head features (85.6% overall accuracy, Kappa = 0.84) (Table 3). Classification accuracy was not substantially affected by subtracting body or head

Table 1 Mean values (± SD) and standard deviation (± SD) values of tri-axial body acceleration, pitch and roll angles and vectorial dynamic body acceleration (VeDBA) during capture and no capture events of nine adult Magellanic penguins *Spheniscus magellanicus* diving along the bottom phase, the ascent phase, the first meters of the water column and inside a shoal

	Bottom			Ascent			First meters			Shoal		
	Capture	No capture	Test	Capture	No capture	Test	Capture	No capture	Test	Capture	No capture	Test
Mean surge (g)	0.31±0.19	0.25±0.16	$t_{38}=0.3$ $p=01$	0.64±0.21	0.64±0.13	$t_{28}=0.03$ $p=0.97$	0.43±0.22	0.46±0.20	$t_{14}=-0.3$ $p=0.8$	0.30±0.20	0.31±0.18	$t_{42}=-0.1$ $p=0.9$
Mean sway (g)	−0.08±0.18	−0.16±0.25	$t_{38}=1$ $p=0.2$	−0.12±0.13	−0.08±0.17	$W=143$ $p=0.2$	−0.26±0.17	−0.21±0.21	$t_{14}=0.1$ $p=0.9$	−0.10±0.18	−0.12±0.20	$t_{42}=0.4$ $p=0.7$
Mean heave (g)	0.63±0.13	0.85±0.07	**$W=38$ $p<0.01$**	0.56±0.32	0.51±0.09	$W=75$ $p=0.13$	0.57±0.24	0.68±0.14	$t_{14}=-1.2$ $p=0.26$	0.58±0.21	0.82±0.09	**$W=43$ $p<0.01$**
Mean pitch angle (°)	22.9±14	15.72±10	$t_{38}=1.9$ $p=0.06$	45±17	48±10	$t_{28}=0.6$ $p=0.5$	34.17±20	30.25±14	$t_{14}=0.4$ $p=0.66$	23.88±13	19.84±12	$W=281$ $p=0.30$
Mean roll angle (°)	−5.04±13	−9.71±15	$t_{38}=1$ $p=0.3$	−7.35±8	−4.85±11	$W=145$ $p=0.18$	−17.3±11	−17.01±13	$t_{14}=-0.04$ $p=0.96$	−7.32±13	−7.7±13	$t_{42}=0.1$ $p=0.92$
Mean VeDBA	0.49±0.23	0.16±0.03	**$W=385$ $p<0.01$**	0.12±0.05	0.49±0.19	**$W=221$ $p<0.01$**	0.55±0.14	0.16±0.09	**$t_{14}=7$ $p<0.01$**	0.60±0.19	0.15±0.05	**$W=478$ $p<0.01$**
SD surge	0.52±0.19	0.18±0.1	**$W=379$ $p<0.01$**	0.17±0.12	0.34±0.12	**$W=192$ $p<0.01$**	0.43±0.12	0.22±0.14	**$t_{14}=3.3$ $p=0.01$**	0.50±0.13	0.19±0.1	**$W=456$ $p<0.01$**
SD sway	0.26±0.1	0.07±0.02	**$W=384$ $p<0.01$**	0.10±0.1	0.30±0.1	**$W=213$ $p<0.01$**	0.30±0.1	0.10±0.06	**$t_{14}=4.7$ $p<0.01$**	0.37±0.15	0.09±0.04	**$W=458$ $p<0.01$**
SD heave	0.47±0.19	0.16±0.04	**$W=390$ $p<0.01$**	0.17±0.1	0.54±0.21	**$W=210$ $p<0.01$**	0.50±0.13	0.17±0.13	**$t_{14}=5.1$ $p<0.01$**	0.55±0.13	0.17±0.08	**$W=479$ $p<0.01$**
SD pitch angle	25.52±13	9.38±7	**$W=360$ $p<0.01$**	10.73±9	19.28±8	**$W=181$ $p<0.01$**	16.14±8	11.76±9	$t_{14}=1.1$ $p=0.3$	21.95±10	9.32±8	**$W=353$ $p<0.01$**
SD roll angle	7.43±3.84	1.7±0.76	**$W=376$ $p<0.01$**	3.88±4.12	8.35±2.52	**$W=205$ $p<0.01$**	6.43±3.26	4.1±3.46	$t_{14}=-0.04$ $p=0.18$	11.66±5.02	2.71±2.55	**$W=449$ $p<0.01$**

Significant statistic values from *t* test and Mann–Whitney Test are indicated in bold. SD=standard deviation
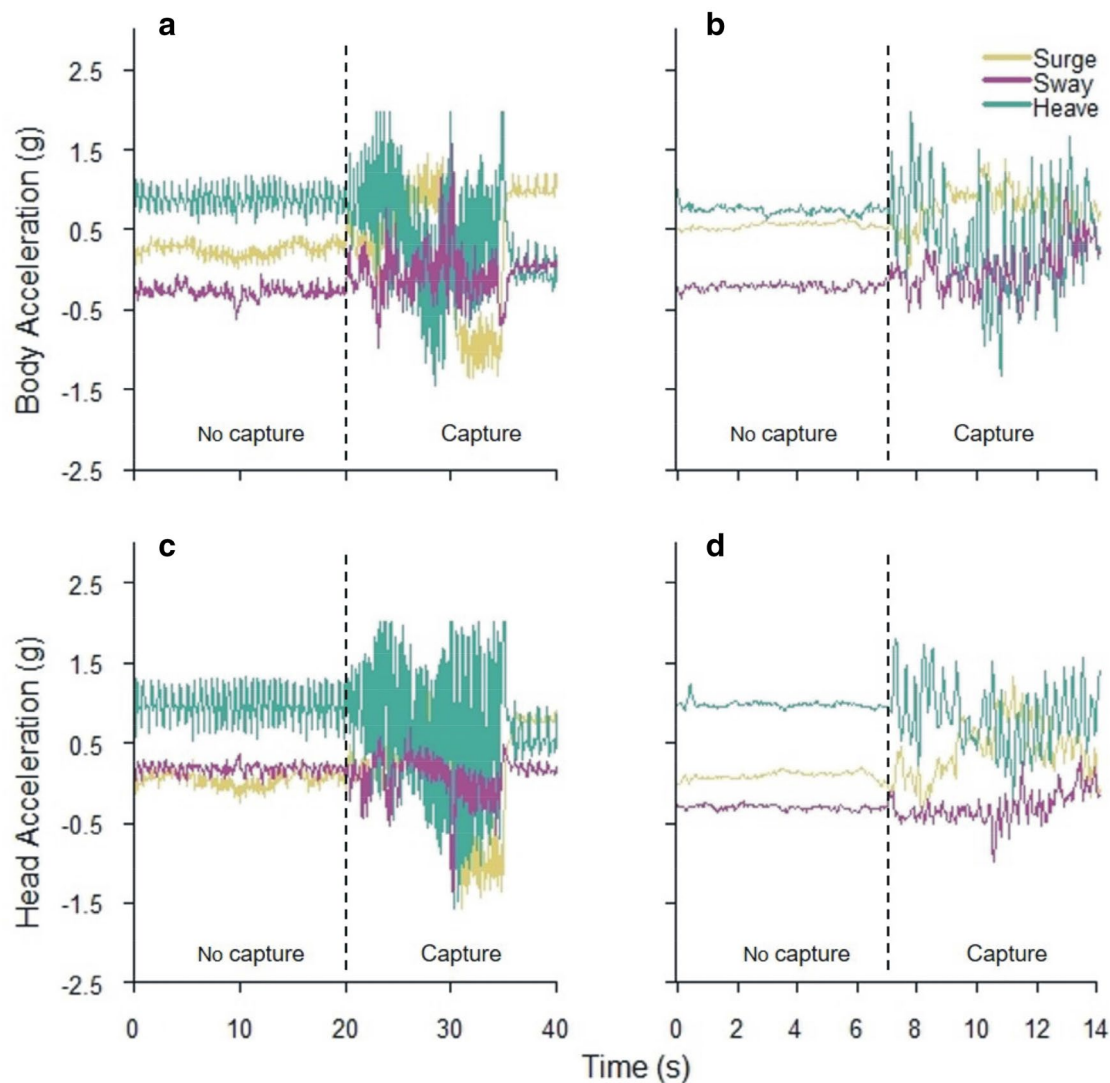
Fig. 3 Example of heave, sway and surge acceleration signals from the body and head of diving Magellanic penguins *Spheniscus magellanicus* during a control period and a prey capture on the bottom phase of a dive (**a** and **c**) and during a control period and a prey capture during the ascent phase of a dive (**b** and **d**)

acceleration features (Table 3). However, sensitivity (fraction of segments correctly predicted as positives for a given class of behaviour) slightly decreased when predictors were subtracted (Table 3). In general, along the three K-NN models, captures presented less sensitivity values than swimming periods (Table 3) and in the three K-NN models, captures that took place during the bottom phase of a dive and inside a shoal had the lower sensitivity values (Table 3).

Prey capture rates

The total amount of captures identified by means of the K-NN algorithm was, in all penguins but one, higher than the amount of captures estimated by means of counting wiggles (Table 4). In these penguins, the K-NN recognized on average 10% (range: 3–16%) and 77% (range: 11–148%) more capture events than those estimated by wiggle identification, for Punta Norte/San Lorenzo and Cabo dos Bahías, respectively. The CPUT when captures were estimated using the K-NN method was similar or higher than that estimated by counting wiggles in four of the five birds from Punta Norte/San Lorenzo (Table 4). However, the CPUT estimated by the K-NN method
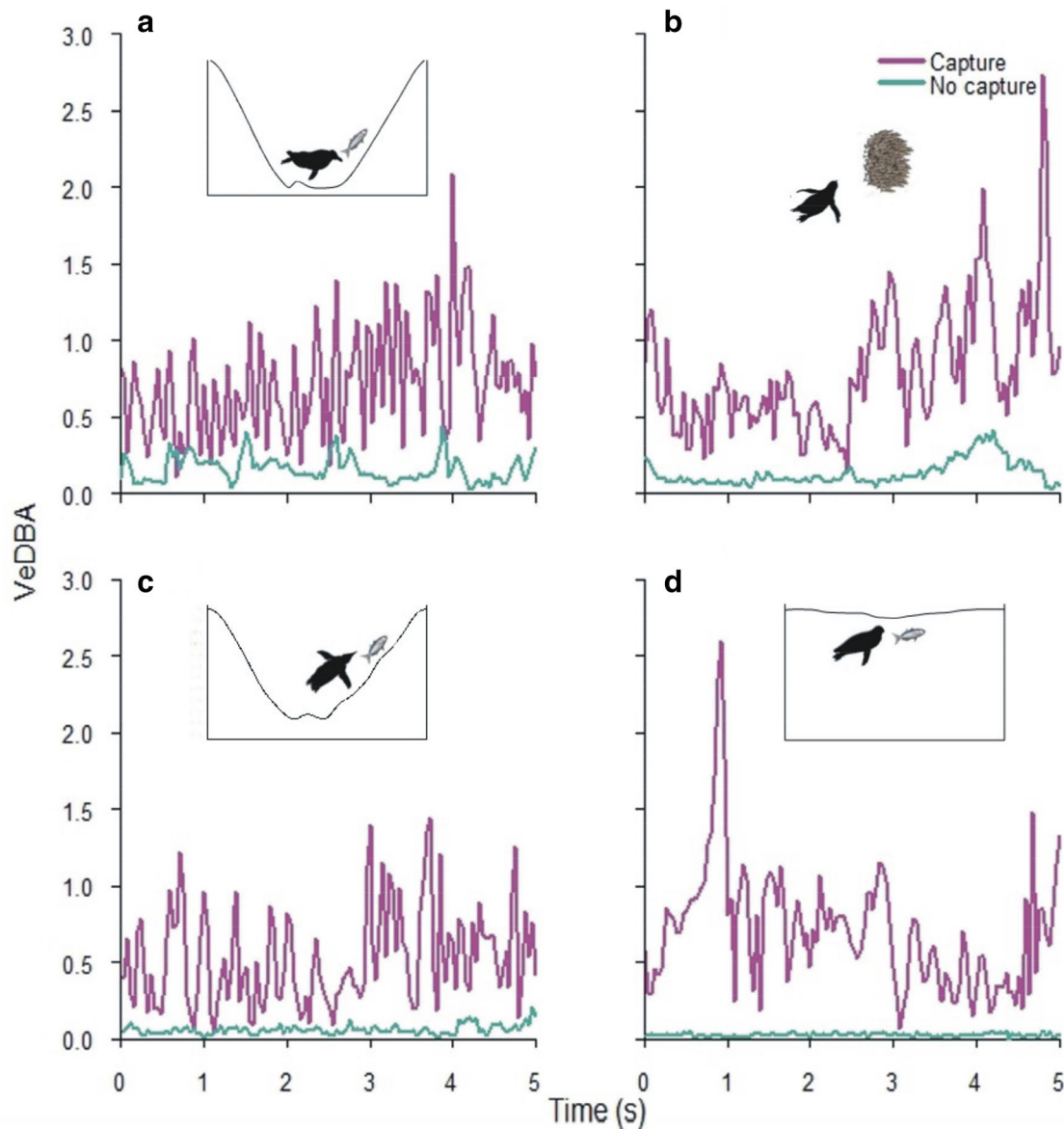
Fig. 4 Vectorial dynamic body acceleration (VeDBA) values during control periods (blue) and prey capture events (violet) on the bottom phase of a dive (**a**), inside a shoal (**b**), during the ascent phase of a dive (**c**) and during the first meters of the water column (**d**)

was higher than that estimated by counting wiggles for the five penguins from Cabo dos Bahías (Table 4).

Discussion

We successfully used the combination of video cameras, depth, head and body acceleration data to determine Magellanic penguins' prey capture events, distinguish different prey capture behaviours and associate each one of them to particular head and body movements.

Of all the acceleration-derived metrics, the standard deviation was the one that differed the most between capture and control behaviours. This finding agrees with previous studies that have already indicated the importance of standard deviation as a good behaviour predictor (Chimienti et al. 2017; Jeantet et al. 2018). Of the three acceleration channels, the dorso-ventral (i.e., heave acceleration signal) showed the greatest variation during capture events in comparison to control periods. This would be principally associated with the increase flipper beat amplitude and frequency necessary to swim faster when penguins approach prey underwater (Watanuki et al. 2003; Kato et al. 2006; Jeanniard-du-Dot et al. 2016). Prey capture events were also characterised by an important variation in the surge acceleration signal (i.e., forward–backward motion) as a consequence of the

Table 2 Mean values (±SD) and standard deviation (±SD) values of tri-axial head acceleration during capture and no capture events of nine adult Magellanic penguins *Spheniscus magellanicus* diving along the bottom phase, the ascent phase, the first meters of the water column and inside a shoal

	Bottom			Ascent			First meters			Shoal		
	Capture	No capture	Test	Capture	No capture	Test	Capture	No capture	Test	Capture	No capture	Test
Mean surge (g)	0.06±0.16	−0.04±0.18	$t_{38}=1.9$ $p=0.06$	0.26±0.15	0.24±0.29	$W=124$ $p=0.65$	0.12±0.19	0.04±0.23	$t_{14}=0.7$ $p=0.52$	−0.02±0.27	−0.07±0.22	$W=262$ $p=0.65$
Mean sway (g)	−0.05±0.18	−0.05±0.22	$W=190$ $p=0.7$	−0.13±0.16	−0.14±0.18	$t_{28}=0.1$ $p=0.94$	−0.19±0.18	−0.20±0.11	$t_{14}=0.1$ $p=0.89$	−0.09±0.20	−0.07±0.22	$t_{42}=-0.3$ $p=0.74$
Mean heave (g)	0.64±0.46	0.73±0.58	**$W=93$** **$p<0.01$**	0.72±0.42	0.73±0.47	$W=97$ $p=0.5$	0.76±0.12	0.89±0.05	**$W=7$** **$p=0.01$**	0.76±0.13	0.92±0.05	**$W=37$** **$p<0.01$**
SD surge	0.50±0.16	0.17±0.09	**$W=384$** **$p<0.01$**	0.39±0.10	0.19±0.12	**$W=199$** **$p<0.01$**	0.48±0.13	0.20±0.13	**$t_{14}=4.1$** **$p<0.01$**	0.48±0.11	0.19±0.1	**$W=460$** **$p<0.01$**
SD sway	0.28±0.13	0.07±0.04	**$W=382$** **$p<0.01$**	0.27±0.09	0.09±0.06	**$W=217$** **$p<0.01$**	0.33±0.12	0.08±0.04	**$W=64$** **$p<0.01$**	0.37±0.12	0.08±0.03	**$W=476$** **$p<0.01$**
SD heave	0.48±0.21	0.22±0.05	**$W=365$** **$p<0.01$**	0.44±0.16	0.17±0.11	**$t_{28}=5$** **$p<0.01$**	0.63±0.14	0.19±0.12	**$W=64$** **$p<0.01$**	0.53±0.13	0.19±0.08	**$W=481$** **$p<0.01$**

Significant statistic values from *t* test and Mann–Whitney Test are indicated in bold. SD = standard deviation
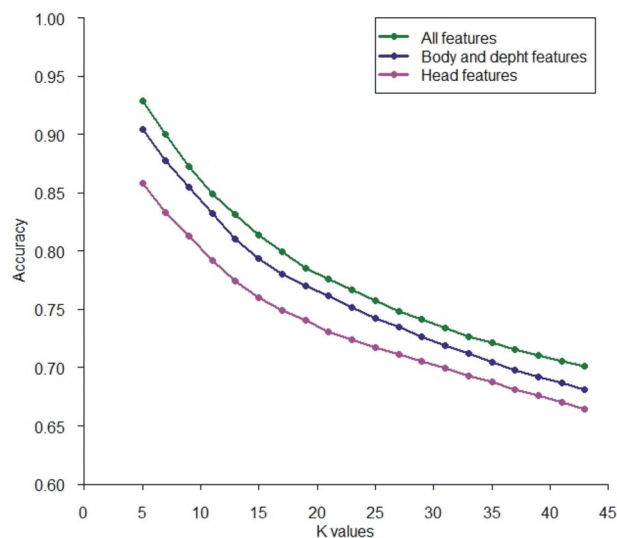

Fig. 5 Change in accuracy according to the K value for each of the three K-Nearest Neighbour (K-NN) models (one including all features, one including the body and depth features and the third one only including the head features)

higher wing flapping frequency and strength that generates a greater forward propulsion (Arai et al. 2000). Finally, the higher oscillations in the pitch and roll angles during captures seemed to be associated to the prey capture strategy described for the Magellanic Penguin which consists in approaching prey from below and tilt the body sideways to change swimming direction rapidly (Wilson and Duffy 1986; Wilson et al. 1987; Rodary et al. 2000; Ropert-Coudert et al. 2001; Takahashi et al. 2004b). All of these results are in line with previous findings which indicate that Magellanic penguins "speed up" to feed on prey that usually travels at similar speeds as penguins, such as anchovy and sardine (Wilson et al. 2002a, b). The similarity in Magellanic penguins' head and body movements would be principally linked to the compact body these birds have (Guinard et al. 2010). The short neck condition and highly hydrodynamic body shape have been deemed to be advantageous features for penguins to reach higher velocities during swimming and to increase capture efficiency (Wilkinson and Ruxton 2012). In addition, the short neck would minimise the body surface area, reducing the loss of heat during the long periods at sea (Wilson et al. 2017).

The application of a simple and easy to implement supervised algorithm such as the K-NN showed accuracy scores above 90% when considering both head and body related features. The high performance of the algorithm is probably related to the marked differences in the standard deviation values as well as in the VeDBA between capture and control behaviours (see above). In general, the three models proposed in this study (i.e., body and head, body only and head

Table 3 Model accuracy parameters for supervised classification by means of K-Nearest Neighbour (K-NN) models of accelerometer and depth data from free living Magellanic penguins *Spheniscus magellanicus*

Model	Diving Phase	Behaviour	Sensitivity	Specificity	Pos. Pred. Value	Neg. Pred. Value	Prevalence	Balanced accuracy
All features	Bottom	Capture	0.85	0.98	0.87	0.98	0.12	0.92
		No capture	0.97	0.99	0.95	1.00	0.12	0.98
	Shoal	Capture	0.85	0.99	0.90	0.98	0.12	0.92
		No capture	0.93	0.99	0.96	0.99	0.13	0.96
	Ascent	Capture	0.91	0.99	0.94	0.99	0.13	0.95
		No capture	0.96	0.99	0.95	0.99	0.14	0.98
	First meters	Capture	1.00	0.99	0.92	1.00	0.12	0.99
		No capture	1.00	1.00	0.98	1.00	0.12	1.00
Body acceleration and depth features	Bottom	Capture	0.81	0.97	0.79	0.97	0.12	0.89
		No capture	0.91	0.99	0.91	0.99	0.13	0.95
	Shoal	Capture	0.83	0.98	0.87	0.98	0.11	0.90
		No capture	0.89	0.99	0.94	0.98	0.13	0.94
	Ascent	Capture	0.92	0.98	0.90	0.99	0.13	0.95
		No capture	0.94	0.99	0.94	0.99	0.13	0.97
	First meters	Capture	1.00	0.99	0.96	1.00	0.12	1.00
		No capture	1.00	1.00	0.99	1.00	0.13	1.00
Head acceleration features	Bottom	Capture	0.75	0.97	0.78	0.96	0.13	0.86
		No capture	0.92	0.98	0.86	0.99	0.12	0.95
	Shoal	Capture	0.77	0.97	0.81	0.97	0.12	0.87
		No capture	0.80	0.99	0.90	0.97	0.13	0.89
	Ascent	Capture	0.79	0.97	0.81	0.97	0.13	0.88
		No capture	0.87	0.98	0.87	0.98	0.13	0.92
	First meters	Capture	0.96	0.98	0.89	0.99	0.12	0.97
		No capture	1.00	0.99	0.93	1.00	0.12	0.99

Parameters are reported for the three proposed models: "All features" which included features derived from the body and head acceleration and depth data; "Body acceleration and depth features" which included only features derived from body acceleration and depth data and "Head acceleration features" which only involved features derived from head acceleration data

only features) performed well to determine prey capture events. However, when prey capture took place at the bottom and inside a shoal, the head-featured model computed less sensitivity. The lack of distinction between these two types of captures when only head data were included in the algorithm would be principally related to the fact that neither VeDBA nor depth features were considered. Moreover, even though we treated these two types of captures as different behaviours they share several characteristics. For example, when capturing prey at the bottom penguins could also be swimming inside a shoal but the low light conditions associated with deep waters precluded us from seeing it. Unfortunately, 36% of the total amount of time penguins spent at the bottom was unusable because of the low light levels, thus a bigger sample size and the development of cameras with a light source is crucial to clarify this particular point.

The high classification accuracy scores obtained by the K-NN algorithm when only body features were considered allowed us to estimate the total captures and the CPUT of 10 foraging birds, and compared them with the amount of captures and the CPUT obtained by means of wiggles in two different colonies. Differences between both methodologies were particularly important at Cabo dos Bahías, where the K-NN algorithm recognized significantly more captures than the wiggle technique. Observed inter-colony differences could be a consequence of a differential prey items/sizes adult breeders from both colonies consume. As mentioned, Magellanic penguins from both colonies (located north of 44° S) are predomintantly monophagic, consuming Argentine Anchovy (Frere et al. 1996; Castillo et al. 2019; Fernandez et al. 2019). However, Cabo dos Bahías is located at the southern limit of the latitudinal range of such main prey item, where inter-annual changes in abundance and/or availability have been observed

Table 4 Number of prey captures and capture per unit effort (CPUT) (±SD) estimated by means of the K-Nearest Neighbour (K-NN) algorithm and by means of counting wiggles (see text) during the foraging trip of 10 Magellanic penguins *Spheniscus magellanicus*

ID	Colony	Method								Test
		K-NN						Wiggles		
		Bottom phase	Inside a shoal	Ascent phase	First meters	Total	CPUT	Total	CPUT	
1	PN	21	83	14	9	127	0.84 ± 0.70	109	0.71 ± 0.32	*z = 2.1* *p = 0.04*
2	PN	244	84	88	66	482	0.77 ± 0.60	545	0.93 ± 0.53	*z = 4.0* *p < 0.01*
3	PN	228	50	56	11	345	0.84 ± 0.46	304	0.68 ± 0.39	*z = −4.5* *p < 0.01*
4	PN	335	82	31	41	489	0.83 ± 0.60	479	0.82 ± 0.63	*z = −0.2* *p = 0.85*
5	PN	341	68	25	38	472	0.74 ± 0.56	436	0.71 ± 0.32	*z = −0.9* *p = 0.30*
6	CDB	145	56	0	16	217	0.74 ± 0.73	196	0.69 ± 0.56	*z = −2.2* *p = 0.03*
7	CDB	304	4	35	8	351	1.02 ± 0.44	186	0.57 ± 0.33	*z = −15.5* *p < 0.01*
8	CDB	219	44	4	1	268	0.79 ± 0.36	227	0.69 ± 0.41	*z = −3.75* *p < 0.01*
9	CDB	332	2	69	26	429	0.79 ± 0.62	173	0.43 ± 0.38	*z = −17.14* *p < 0.01*
10	CDB	181	83	26	5	295	0.44 ± 0.53	134	0.27 ± 0.11	*z = −18.5* *p < 0.01*

(Hansen et al. 2001). Such site-specific variability would be responsible for the high inter-seasonal variation in the foraging and diving behaviour of Magellanic penguins from this particular colony (G. Blanco and F. Quintana unpubl data). It is reasonable to think that, under these fluctuations in anchovy abundance and availability, penguins from Cabo dos Bahías would be consuming alternative sizes of their main prey or even different prey items that would not necessarily imply a wiggle leading, in this way, to an important difference in the CPUT estimated by both methodologies.

In conclusion, records of tri-axial body acceleration data present an easy and accurate tool to determine prey capture events in the Magellanic Penguin and probably other penguin species of the genus *Spheniscus* that principally feed on schooled pelagic fish (Wilson and Wilson 1990). As an advantage over wiggles, accelerometer data not only offers the opportunity to identify different types of prey capture behaviours but also to estimate the energy expenditure associate to each capture via VeDBA or ODBA metrics (Wilson et al. 2019). In summary, from a methodological point of view, our study makes an important contribution to improve the knowledge of the trophic ecology of this species and provides an alternative and precise way of estimating prey consumption in other related diving seabirds.

Availability of data and material The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval All penguin handling procedures were reviewed and approved by the Dirección de Fauna y Flora Silvestre and the Ministerio de Turismo y Áreas Protegidas de la Provincia de Chubut (permits to work at Punta Norte during 2015 and 2016: No. 096-SsCyAP/15 and No. 096-SsCyAP/16, permit to work at Cabo dos Bahías during 2015:

No. 075-SsCyAP/15). During instrumentation, birds were handled as quickly and efficiently as possible.

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