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DOI

[10.19227/jzar.v8i4.522](https://doi.org/10.19227/jzar.v8i4.522)

Publication date

2020

Document Version

Final published version

Published in

Journal of Zoo and Aquarium Research

License

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[Link to publication](#)

Citation for published version (APA):

Nuijten, R., Prins, E. F., Lammers, J., Mager, C., & Nolet, B. A. (2020). Calibrating tri-axial accelerometers for remote behavioural observations in Bewick's swans. *Journal of Zoo and Aquarium Research*, 8(4), 231-238. <https://doi.org/10.19227/jzar.v8i4.522>

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Research article

Calibrating tri-axial accelerometers for remote behavioural observations in Bewick's swans

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Keywords: animal behaviour, classification model, conservation, *Cygnus columbianus bewickii*, foraging, random forest

Article history:

Received: 05 Feb 2020

Accepted: 02 Apr 2020

Published online: 31 Oct 2020

Abstract

Accelerometers in tracking devices are increasingly used to identify behaviour leading to detailed insights into the lives of free-ranging animals. To make proper use of an accelerometer, their settings and signals need to be tested and calibrated. Calibration of an accelerometer can be done by directly observing an individual animal of the species of interest, while an accelerometer is simultaneously measuring the movements of this individual. In case direct observations are difficult to obtain, this procedure can be performed with captive individuals. This study sought to calibrate the accelerometer sensor in GPS/GSM neck-collars in Bewick's swans *Cygnus columbianus bewickii* with observations of captive individuals in three zoos in the Netherlands. Using a random forest classification model, five behavioural classes were classified with an overall accuracy of 91%. An additional behavioural class (aquatic foraging) was identified based on a water sensor that was also included in the GPS/GSM collars. This classification was subsequently applied to accelerometer data from 12 free-ranging Bewick's swans equipped with these neck-collars to identify their behaviour during two spring migrations (2017 and 2018). The resulting time-activity budgets were in general agreement with current knowledge based on fragmentary field observations of Bewick's swan flocks along the flyway. The study shows how observations of zoo individuals can be instrumental to derive time-activity budgets of free-ranging individuals that can contribute to further research into the ecology of the species.

Introduction

Rapid technological developments make it possible to not only track the location of individual animals, but to also observe their behaviour remotely by including an accelerometer in the tracking device (Kays et al. 2015). The accelerometer is a sensor that measures acceleration, usually in three directions, that are referred to as x (surge), y (sway) and z (heave) (Yoda et al. 2001). By correctly interpreting the resulting data, the behaviour of free-ranging individuals at the moment of measurement can be deduced. The use of an accelerometer for remote observations is particularly valuable in species that are elusive or have a hidden lifestyle, such as marine or nocturnal species. Migratory animals form a special group in this respect,

since a species might be more easily within range of direct observation in one season than in another.

Just as the remote tracking of animals can reveal astonishing journeys by some individuals (for example in bar-tailed godwits *Limosa lapponica baueri*; Gill et al. 2009), the use of accelerometers has yielded surprising insights into the lives of free-ranging animals. Accelerometer data confirmed that common swifts *Apus apus* stay airborne >99% of the time for 10 months every year in the non-breeding season (Hedenström et al. 2016). By identifying prey captures from accelerometer data, it was found that foraging success in little penguins *Eudyptula minor* is reduced with higher sea surface temperatures, which are expected to occur more frequently in the future (Carroll et al. 2016). In contrast, accelerometer data revealed that part of

the East Atlantic flyway population of brent geese *Branta bernicla* seem to profit from their changing environment: individuals foraging on nutritious agricultural grassland pastures spent less time foraging, but nevertheless were able to advance their migration and arrive earlier at breeding grounds compared to conspecifics foraging on natural salt marshes (Dokter et al. 2018). Such findings can help understand the ecology of species and their ability to cope with changes in their environment.

Accelerometers are demanding sensors in terms of logging capacity, since three numbers (x/y/z) are collected at high frequency. This is usually why accelerometers do not measure acceleration continuously but record data in short 'bouts' (an exception are the daily diaries described in Wilson et al. 2008). Choosing the appropriate settings (e.g. number of bouts per day, duration of bouts and the frequency of measurements within the bout) is important, because when not done correctly, it may become practically impossible to accurately deduce the behaviour of the animal from the data. The settings can have different optimums for different species (Pagano et al. 2017) and tracking devices (Kölzsch et al. 2016), which is why it is essential to test and calibrate the accelerometer with live observations before the start of the study.

Calibration of the accelerometer can be done by directly observing an individual animal of the species of interest, while an accelerometer is simultaneously measuring the movements of this individual. By matching the pattern of the x/y/z data with the observed behaviour in time, the pattern can be classified as such. Classification algorithms or machine learning can then be used to create a classification model in order to annotate acceleration data from free-ranging individuals with a specific behaviour (Shamoun-Baranes et al. 2012).

Next to an accelerometer, other sensors can also be incorporated into tracking devices to learn about animal behaviour and the interaction of individuals with their environment. Some sensors measure internal variables such as heart rate (Duriez et al. 2014; Wascher et al. 2018), while others measure environmental variables such as temperature (Ryan et al. 2004; Sala et al. 2017). A less well-known sensor is the conductivity sensor. This sensor measures the conductivity of its surroundings and can be used to map aquatic environments (Hussey et al. 2015) or, for example, to assess the hunting circumstances for predatory electrogenic fish (such as electric eel and knifefish; MacIver et al. 2001). Because conductivity in air and water differs substantially (Pagano et al. 2017), the sensor can also be used to detect when a device (and thus an individual) is submerged in water; which can be particularly useful in terrestrial animals that frequently swim or dive to forage.

Bewick's swan *Cygnus columbianus bewickii* is a large-bodied, migratory bird that winters in northwest Europe and breeds at the European-Russian tundra. The species makes several stop-overs to complete its migratory journey, where it feeds to fuel its migration and also in spring to gain reserves for breeding (Beekman et al. 1991; Beekman et al. 2002; Nolet 2006; Nuijten et al. 2014). Since 1995, the species has been declining rapidly for unknown reasons but supposedly because of changes during their spring migration. To understand this, this study sought to gain insight into the behaviour of Bewick's swans during the spring migration. Therefore, free-ranging Bewick's swans were equipped with tracking devices with built-in accelerometer and water sensor.

Captive Bewick's swans in three zoos were used to test the accelerometer settings, calibrate the accelerometer sensor, and to derive a model to classify acceleration measurements from individual Bewick's swans into relevant behaviours. To illustrate how observations in captive animals contribute to research on free-ranging animals, this paper presents an application of the classification model to ACC data from free-ranging Bewick's swans during the spring migrations in 2017 and 2018.

Table 1. Ethogram that was used for the observations of captive swans in 2016 and 2017. Both individuals were observed simultaneously where possible, otherwise one of the individuals was recorded as being 'out-of-sight' (x).

Behaviour	Behaviour
Swimming	Aquatic foraging (up-ending)
Walking	Trampling
Standing alert	Surfacing
Standing relaxed	Drinking
Sleeping (head curled)	Wing flapping
Preening feathers	Vocalising
Preening collar	Vigilance/Interaction with keeper
Terrestrial foraging	Other
Aquatic foraging (neck down)	Out-of-sight

Methods

Behavioural observations

In summer 2016 and autumn 2017, behavioural observations were carried out in three zoos in the Netherlands. In total, four different Bewick's swans, two males and two females, all with clipped wings, were observed for 38 hr (2016: 18 hr; 2017: 20 hr). First, the swans were equipped with a specifically designed, 3D-printed white GPS/GSM neck-collars with black alpha-numeric code to allow for individual recognition. The collar weighed about 70 g, with an inner diameter of 51 mm and a height of 80 mm. Previous observations with a similar sized collar showed that wearing of the collar did not affect the swans after four weeks, but during the first four weeks the swans were observed to preen more than their conspecifics without the collar (Nuijten et al. 2014). As the proportion of time spent on each of the behaviours in the captive individuals was not of interest, observations began one day after deploying the device.

The collar contained a tri-axial accelerometer (Brown et al. 2013) and a water sensor, and sent its data remotely via the GSM network to a server on a daily basis. The water sensor measures conductivity, which is different in water than in air (Pagano et al. 2017). Two conductivity sensors were placed on the collars of the swans: one on the top left and one on the bottom right, to maximise the distance between them. Only if both sensors are submerged, will the sensor give a positive signal ('1'). Bewick's swans submerge their neck when feeding aquatically (Brouwer and Tinbergen 1939), so this behaviour was considered an indicator of aquatic foraging.

In summer 2016, two Bewick's swans were observed in Burgers' Zoo (5 yr female, 14 yr male) and two in Stichting Vogelpark

Table 2. List of the 20 summary statistics used in the random forest analysis as predictors for the classification of the acceleration data.

#	Name	Calculation	Description
1, 2, 3	mean_x, mean_y, mean_z	Mean(x y z)	Mean of x y z; also called 'static acceleration' (Watanabe et al. 2005; Shamoun-Baranes et al. 2012)
4, 5, 6	sd_x, sd_y, sd_z	sd(x y z).	Standard deviation of x y z
7, 8	min_z, max_z	Min(z), max(z)	Minimum z-value within bout. Only in z-direction as the neck-collars for the swans can turn and therefore the orientation of the x and y axis cannot be reliably known (Watanabe et al. 2005)
9, 10, 11	odba_x, odba_y, odba_z	$\sum MA(x y z)$	Sum of the differences between the x y z measurement and the static acceleration, here calculated as the sum of the moving average with a width of 8 (Shamoun-Baranes et al. 2012)
12	ODBA	odba_x + odba_y + odba_z	Sum of odba in all directions (Shamoun-Baranes et al. 2012)
13	meanslope_z	Mean($\sum((z[n] - z[n-1])/1)$)	Mean slope of z between two measurements
14	sdslope_z	Sd(meanslope_z)	Standard deviation of the slope of z
15	sumslope_z	$\sum(\text{meanslope}_z)$	Sum of the slopes of z
16, 17, 18	sumtrans_x, sumtrans_y, sumtrans_z	$\sum(\text{ifelse}(x[n] < \text{mean}(x y z) \& \text{mean}(x y z) < x[n+1], 1, 0))$	Number of times x crosses meanx, proxy for periodicity of signal. Substitute for more demanding (in terms of energy for calculation) Fast Fourier Transformation
19	meanvectorlength	Mean($\sqrt{(x[n]^2 + (y[n]^2 + z[n]^2))}$)	Mean vector length for x, y and z
20	sdvectorlength	sd($\sqrt{(x[n]^2 + (y[n]^2 + z[n]^2))}$)	Standard deviation of vector length for x, y and z

Avifauna (20 yr female, 10 yr male). In Burgers' Zoo, the swans were housed in a circa 10x20 m single species enclosure with a small pond. They had a small shelter in the back and were fed once a day with pellets. In Stichting Vogelpark Avifauna, the Bewick's swans roamed freely in between the zoo visitors around a large pond. A camera attached to a laptop was used to record the swans, and the behaviour of the swans was recorded continuously using the software programme ObserverXT (Zimmerman et al. 2009). The programme automatically matches video recordings and behavioural observations in time. Both animals were observed simultaneously where possible. In the ethogram, 16 categories of behaviour were distinguished, plus two additional categories for 'other' and 'out-of-sight' (Table 1). The acceleration sensor in the collar measured the acceleration in three directions every 10 sec, with a bout length of 5 sec and measurement frequency of 20 Hz.

In 2017, observations were made of two Bewick's swans in GaiaZOO. These were the same two individuals that were observed in Burgers' Zoo the year before, as they moved between observation periods. In GaiaZOO, the swans were housed in a hilly enclosure of circa 40x40 m which they shared with red pandas *Ailurus fulgens*, Chinese muntjacs *Muntiacus reevesi* and common shelducks *Tadorna tadorna*. A slightly different design was adopted, as ObserverXT was not available in 2017 and the 2016 observations had shown that a bout length of 2 sec was sufficient to capture specific behaviours of the swans. In 2017, point observations were used: every 30 sec the behaviour of the focal animal(s) was recorded and at the same synchronised timepoint the accelerometer also took a measurement. Similar to 2016, the measurement frequency of the accelerometer was 20 Hz and both animals were observed simultaneously where possible.

For the analysis, the duration of the bouts from the 2016

observations was also reduced to 2 sec by taking the first two seconds of every bout. The behavioural observations could be matched exactly with the acceleration data for both years. Bouts that could not be unambiguously linked to a behavioural category, because for example two behaviours were observed within one bout, were removed from the classification.

Summary statistics

In order to find identifiers in the accelerometer data, and to recognise behaviours based on these patterns, 20 different 'classifiers' or summary statistics were calculated from the x, y and z data (Table 2). Most of these summary statistics have been used successfully in other studies before and are described there (see references in Table 2). The Fast Fourier Transformation is often used to detect periodicity (Watanabe et al. 2005), but for computational reasons (the summary statistics were calculated on board of the tracking device; Nuijten et al. 2020) this was not feasible here. Instead, one type of statistic was used that has, to the authors' knowledge, not been used before: the 'sumtrans' statistic. For this statistic, the number of times the signal (x, y or z) crossed its own bout mean was calculated as an indication of the periodicity or repetition in the signal.

Classification and annotation: random forest analysis

There are different methods available for behavioural classification. Random forest is a user-friendly option that had the highest accuracy scores in a direct comparison with four other methods (Nathan et al. 2012). After annotating the accelerometer data with the simultaneously observed behaviours, and creating behavioural classes of interest from the ethogram (see Results), this ensemble learning decision tree method (random forest;

Liaw and Wiener 2002) was used to build a classification model. Observation data were complemented with data from free-ranging flying Bewick's swans (272 observations), as inferred from the GPS signal (location and speed), in spring 2017, as this behaviour could not be observed in the captive individuals.

The dataset was split randomly into a training (60%) and test (40%) dataset to build the classification model and 500 simulations were run. All summary statistics were included as potential explaining variables (Table 2). In order to check the predictive ability of the model, overall classification accuracy (i.e. proportion of correct predictions), sensitivity/recall, specificity and the Matthews correlation coefficient (Chicco 2017; Pagano et al. 2017) were calculated. The latter is regarded to be a better indicator of classification performance when classes are of different sizes, such as in the present case.

Aquatic foraging was not included in the final classification model, as this behaviour was not represented in the captive situation. This behaviour was kept as a behavioural class but was classified based on the water sensor information only. This meant that whenever the water sensor gave a positive signal ('1'=water detected), the annotation of the behaviour for that bout was overruled and changed into aquatic foraging. The accuracy of the water sensor was assessed separately (see Appendix A).

Activity budget during spring migration

In winter 2016/2017, 30 free-ranging Bewick's swans were equipped with a GPS/GSM neck-collar as described before. The sampling frequency of the different sensors was dependent on season and the energy level of the device (Nuijten et al. 2020). The individuals that provided complete accelerometer data for the whole spring seasons of two subsequent years (2017 and 2018) were selected, and time-activity budgets were compared between the seasons based on the final classification. This resulted in a dataset of two spring seasons from 12 adult female swans. GPS positions were taken every 15 min, ACC measurements every 2 min (with a bout duration of 2 sec, and bout frequency of 20 Hz) and water sensor every second (binary). The classification yielded time-activity budgets per individual per year in which all ACC datapoints were annotated with one of the five classified behaviours (Table 3).

Table 3. Final behavioural classes in the annotation of the accelerometer data of free-ranging Bewick's swans in spring 2017 and 2018. The first five behaviours were classified based on the random forest analysis, the sixth behaviour is classified based on the water sensor data.

Behaviour	Key in Table 4
Sleeping	SL
Standing	ST
Swimming	SW
Terrestrial active	TE
Flying	FLY
Aquatic foraging	AQ

To classify aquatic foraging, information from the water sensor was used. First the water sensor data were aggregated to batches of 5 min. These aggregates (i.e. 300 sec) were aligned to the ACC data based on the satellite timestamps of both measurements. For every 5 min period, it was specified whether water was detected (a total of >30 sec '1' in raw water sensor data) or not (>270 sec '0' in raw water sensor data). If water was detected, the overlapping ACC bouts were assigned a '1', otherwise a '0' for this statistic.

The annotated ACC bouts from spring migration data were visualised in time-activity budgets. Spring migration season was delimited as the period between 1 February and 25 May (114 days). The former was chosen to ensure the inclusion of the preparatory fueling phase (Beekman et al. 2002); the latter was found to be a potential 'optimal arriving date' for Bewick's swans in the breeding grounds (Nuijten et al. 2014). Additionally, the proportion of time per day for the two foraging behaviours (terrestrial and aquatic) was calculated and compared between seasons.

Table 4. Confusion matrix with predicted values for the test dataset, abbreviations for behaviours are given in Table 3. Below the matrix are the performance statistics of the random forest classification model per behavioural class calculated based on true positive (TP), true negative (TN), false positive (FP) and false negative (FN) predictions.

Confusion matrix		SL	ST	SW	TE	FLY
Prediction ↓	Reference →					
SL		319	7	0	1	0
ST		9	516	6	59	0
SW		0	10	50	14	0
TE		1	25	4	428	0
FLY		0	0	0	0	104
Performance statistics		SL	ST	SW	TE	FLY
Sensitivity/recall =TP/(TP+FN)		0.9755	0.8746	0.6757	0.9345	1
Specificity =TN/(TN+FP)		0.9918	0.9567	0.9932	0.9324	1
Matthews correlation coefficient =((TP * TN)-(FP * FN))/√((TP+FP)*(TP+FN)*(TN +FP)*(TN+FN))		0.9652	0.8410	0.7394	0.8452	1

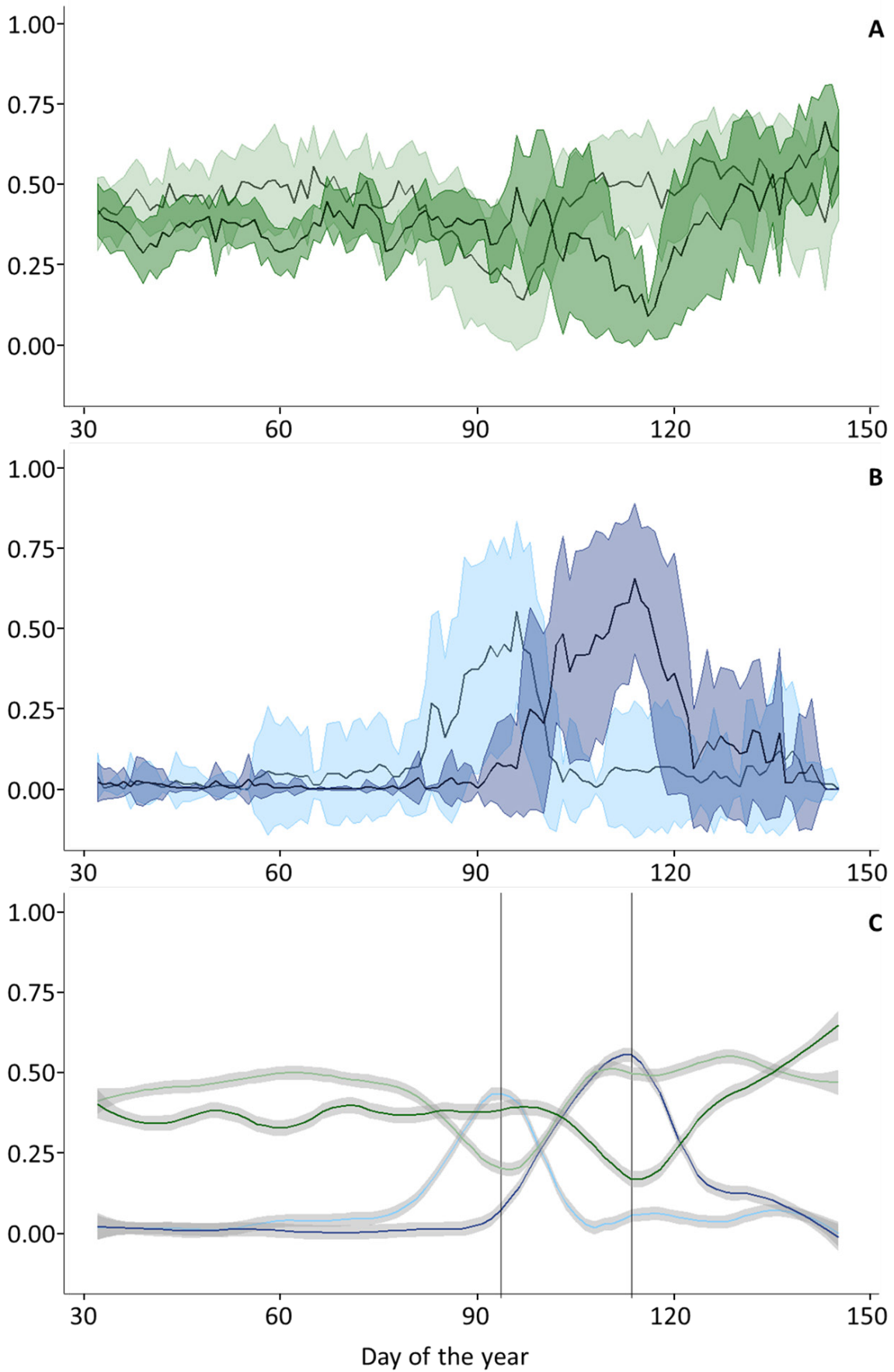


Figure 1. A: average (line) and SD (ribbon) of daily proportion of terrestrial active during spring migration of 12 free-ranging Bewick's swans. Light green is 2017, dark green 2018. The same individuals were tracked in both years. B: average (line) and SD (ribbon) of daily proportion of aquatic foraging during spring migration of 12 free-ranging Bewick's swans. Light blue is 2017, dark blue 2018. The same individuals were tracked in both years. C: smoothed regression lines (Loess regression) of data in Figure 1A and 1B of both years combined. Vertical lines represent the peaks in aquatic foraging for 2017 (left) and 2018 (right).

Results

From ethogram to behavioural classes

The original behaviours identified during the observations (Table 1) were grouped into eight biologically relevant behavioural classes: sleeping, standing alert, standing relaxed, walking, swimming, preening, terrestrial foraging and aquatic foraging. These together contained >95% of the total observations. Two static behaviours, standing alert and standing relaxed, were combined into one class ('standing'), as the difference between them (a neck straight indicating alertness compared to a more curved neck) was arbitrary and proved difficult to distinguish sometimes during the observations. The third static behaviour, sleeping (i.e., head tucked), gave a unique signal and accounted for a large proportion of the data, so this remained a category of its own. Walking and terrestrial feeding were combined in the category 'terrestrial active', as it was noticed that the majority of walking performed by Bewick's swans is in combination with feeding. Preening feathers and preening collar were initially observed as separate behaviours based on the idea that preening of the collar would give more extreme values for x, y and z (not only caused by the movement of the neck but also of the collar itself, while the swan was plucking it). This turned out not to be the case, and because of the similarity between the two preening behaviours, classification was more accurate when combining the two.

In the captive swans, preening took up a large proportion of the day (as was expected since the swans were only given the collar one day before observations started). To prevent this from having an effect on the classification, preening time was reduced to 10% of the total, as was observed in free-ranging Bewick's swans during their migration (Nolet et al. 2001; Nolet and Klaassen 2005; Nolet et al. 2007). In a test version of the classification model, it was clear that terrestrial foraging was often mistaken for preening; therefore, it was decided to include the preening into the behavioural class terrestrial active. This means that in the final results, it will not be possible to distinguish between these behaviours, but it will be possible to estimate the total time a swan spent on them combined. Eventually, six behavioural classes were identified, of which five were classified in the classification model and one (aquatic foraging) was annotated based on the water sensor data (Table 3).

Classification model

The five behavioural classes used in the random forest classification model were classified with an overall accuracy of 91.2% (89.7–92.6, 95% CI). There were some differences between the behaviours in the accuracy of the prediction (Table 4). Flying (FLY) was predicted with a 100% accuracy, while swimming (SW) proved to be much more difficult to predict correctly (69%). Swimming was mostly confused with terrestrial active and standing (Table 4). Not all summary statistics were important for the classification (Appendix B). The three most important statistics were maximum z-value, mean z-value, and ODBA. Based on those three values alone, the accuracy of the classification for the five behaviour classes would still be 91.0% (Appendix C). Since a selection for valuable summary statistics is beyond the scope of this study, all summary statistics were retained in the final model.

The final classification model was applied to two years of spring migration data from 12 free-ranging female Bewick's swans (Appendix D). After classification by the final classification model, the annotation was overwritten by aquatic foraging (AQ) if the water sensor detected water at that point in time. In 90% of cases, a terrestrial active classification was overwritten, followed by 5% for swimming, 4% standing and <0.5% for both sleeping and flying.

Foraging during spring migration 2017 and 2018

Applying the classification model to ACC data from free-ranging Bewick's swans yielded detailed time-activity budgets during the spring migration in two consecutive years (Appendix D). There was a particular interest in foraging behaviours (both terrestrial and aquatic) and whether this would differ within individuals between seasons. A clear pattern of alternation between terrestrial and aquatic foraging was observed over the course of the spring migration season (Figure 1A and B). Despite considerable variation both among and within individuals (Appendix D), a distinct shift in this alternation was visible when comparing both seasons. In spring 2017, the peak of aquatic foraging occurred at day 93 (3 April; Figure 1C) while in spring 2018 this was 20 days later (23 April; Figure 1C). With these peaks, coinciding troughs were visible in terrestrial activity at days 94 (4 April) and 113 (23 April) for 2017 and 2018, respectively. In total, the swans foraged (terrestrial and aquatic foraging combined) for 61.0 days in 2017 and 56.2 days in 2018 out of the 114 days of spring migration analysed here.

Discussion

It was possible to classify the behaviours of Bewick's swans with high accuracy. The high accuracy for flying was not surprising, as other studies also show that this behaviour is characterised by high dynamic body acceleration (Bishop et al. 2015; Shamoun-Baranes et al. 2012; 2016). The behaviour with the lowest accuracy, swimming, was noticed during the observations to be performed in different forms. Fast swimming, for example, was different from slow swimming in terms of neck movements (and thus collar movements detected by the accelerometer). The differences in swimming speed were partly due to differences in the enclosures. In Burgers' Zoo and GaiaZOO, the swans only had a small pond to bath, while in Stichting Vogelpark Avifauna the swans had the opportunity to swim for larger distances, which they sometimes did when they were for example chased by other waterfowl in the enclosure. This variation could have resulted in lower accuracy compared to other behaviours. Despite the lower accuracy, it was decided to keep swimming in as a single behaviour. It was assumed that swimming conditions in free-ranging Bewick's swans would also be very variable, as the swans frequently commute on open (sea) waters with waves from the tide and/or the wind. Having an already diverse practice dataset on which to build the model might thus actually be beneficial.

Although behavioural classification based on an accelerometer sensor may yield a sophisticated proxy for the actual behaviours performed by an individual, the interpretation may differ from when behaviour is derived from direct observations. In direct observations in the field, the environment in which this behaviour is executed can also be recorded and taken into account in the interpretation and analysis. This is true for both the ecological environment (e.g., is a swan walking on a steep slope or slippery underground?) and the social environment (is a certain interaction causing specific behaviour to take place?) of the individual. With remote recordings of acceleration as a proxy for behaviour, these types of additional information are often not available. Additionally, while there is space for scoring 'out-of-sight' or 'other'/'unknown' as a behaviour in real-life focal observations with the option to omit these observations for later analysis, the accelerometer provides data for all measuring bouts, regardless of the context, including those where behaviour is not unambiguous. When applying the classification model to data from free-ranging (unobserved) individuals, every measuring bout is classified as one of the behaviours in the model, thereby ignoring all other behaviours that might have taken place but that were not in the classification model. Despite the fact that this sounds rather non-

nuanced, the choices for the behavioural classes of interest can ensure that much of the behaviour is captured in the model. In this case, for example, more than 95% of all observations in the zoo were represented in the five behavioural classes that were used in the model. If this is assumed to be fully representative of the situation in free-ranging individuals, it would mean that five percent of the accelerometer data is falsely classified as one of the behavioural classes. This aspect of remotely observing behaviour by using an accelerometer is usually neglected, since the overall patterns can still be studied.

In this case, the agreement between the individual time-activity budgets created from the ACC data (Appendix D) and knowledge from field observations of flocks of swans provided confidence in the classification. First, the daily roost flights during dusk and dawn were well detected (Nolet et al. 2002; Nuijten et al. 2020); so well that the time-activity budgets clearly show the increasing day length during spring time (Appendix D). Second, most of the terrestrial active behaviour took place during the day (Appendix D), and resting/sleeping during the night, which is appropriate in diurnal animals such as the Bewick's swan. Third, it was found that the periods in which aquatic foraging took place throughout the day, were when the swans were staging in the Baltic states, foraging in the bays or Estonia, or near the White Sea in Russia in the estuary of the Northern Dvina River (Nolet et al. 2001; 2007; Nolet and Klaassen 2005; Nuijten et al. 2020). Outside these periods, when the swans tend to sleep on water, aquatic foraging was mainly restricted to the night (Nolet et al. 2002; Appendix D).

When looking at the proportion of time the swans spent foraging, it was noticeable that, despite considerable variation within and between individuals, a clear pattern was visible in both years (Figure 1). The swans mainly foraged on terrestrial food sources, except for a period during their migration where they switch to aquatic resources. Comparison with GPS data shows this took place in Estonia and the Dvina Bay in Russia (Nuijten et al. 2020). Further north of these sites, closer to the breeding grounds, the swans return to terrestrial sources. Total foraging time seems to increase as spring progresses in May.

Calculating the total time spent foraging during the 114 days of spring migration included in this study, it was striking that this covers approximately half of the total time (61 days in 2017 and 56 days in 2018). Even if part of the terrestrial active category is preening (probably around 10%; Nolet et al. 2001; 2007; Nolet and Klaassen 2005), this is a considerable amount of time that the swans need to arrive at their breeding grounds on time and with the necessary reserves to initiate breeding (Nuijten et al. 2014).

Further analysis of this type of data, which is beyond the scope of this study, can answer a whole range of questions, for example about the effects of disturbances on foraging time and energy expenditure of individuals (Linssen et al. 2019) or the feasibility of the migration strategy of Bewick's swans under varying environmental conditions (Lameris et al. 2017). These findings can eventually be used to model the annual cycle of a species and yield insights into carry-over effects and potential fitness consequences (van Wijk et al. 2017).

Results such as these can only be derived with detailed knowledge of the behavioural repertoire of individual animals. In many species, it is not possible to acquire this from wild individuals, and captive individuals can offer a solution. It is often questioned whether the behaviour of captive animals is representative of the behaviour of free-ranging conspecifics (Veasey et al. 1996). At least for the current purpose, it is argued that it is, although the behavioural repertoire might be smaller or larger than in free-living conspecifics. This study shows how observations of zoo animals can be instrumental to derive time-activity budgets of free-ranging individuals that in turn facilitate further research into the ecology of the species.

Acknowledgements

We thank all persons that have contributed to the observations in the zoo (Peter de Vries, Nina Thierij, Stefan Vriend, Anne-Lieke Knaven, Roxan Havik) and all the keepers who helped with the handling, and everyone who helped with the catching and ringing of the free-ranging Bewick's swans (Gerard Müskens, Youri van der Horst, Erik Kleyheeg, Peter de Vries, Thomas Lameris, Chiel Boom, Robert van der Meer, Anna Hermsen, Jan Vegelin, Fred Cottaar). We acknowledge the Royal Burgers' Zoo in Arnhem, Stichting Vogelpark Avifauna in Alphen aan den Rijn and GaiaZOO in Kerkrade for their permission to test the GPS/GSM collars and observe the captive Bewick's swans in their institutions. The field study was approved by the Centrale Commissie Dierproeven (license 2016518), and licensed by exemptions Flora- en Faunawet 75A obtained through Dienst Regelingen (FF/75/2016/044). We thank an anonymous reviewer for constructive comments on earlier versions of the manuscript. RJMN was supported by NWO-NPP grant 866.15.206.

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