

RESEARCH

Open Access



Prey ingestion rates revealed by back-mounted accelerometers in Eurasian spoonbills

Tamar Lok^{1*†}, Matthijs van der Geest^{2,3†}, Roeland A. Bom¹, Petra de Goeij³, Theunis Piersma^{1,3} and Willem Bouten⁴

Abstract

Background Quantifying foraging success in space and time and among individuals is essential for answering many ecological questions and may guide conservation efforts. However, collecting this information is challenging for species that forage on mobile prey and are difficult to observe visually, for example, because they forage in inaccessible areas or at night. In such cases, the use of tracking devices that simultaneously collect location and acceleration data may provide a solution if foraging success can be extracted successfully. The aim of this study was to assess how well searching for and ingesting prey, among other behaviours, could be distinguished from 20 Hz acceleration data collected by GPS/ACC-trackers mounted on the back of Eurasian spoonbills *Platalea leucorodia*. Upon capturing a prey, spoonbills make a distinct movement with their head and back to throw the prey from the tip of the bill into the throat.

Methods We compared the behavioural classification performance of random forest models that were trained and tested on video-annotated acceleration data segments of different (fixed or flexible) lengths. The best-performing model was then applied to 4 years of data of spoonbills foraging in the Wadden Sea during the breeding season, to explore seasonal and annual variation in prey ingestion rates.

Results Highest classification accuracies (as indicated by the F-measure, a balanced measure of precision and sensitivity) of foraging behaviours were achieved by analysing short fixed-length segments (0.4–0.8 s) or “flexibly-cut” segments. The F-measure was very high (> 0.90) for searching, standing, sitting and flying (distinguishing active and passive flight), 0.73 for ingesting prey and 0.65 for walking. False positive and negative prey ingestions were equally likely and most often confused with searching, resulting in a close match between the predicted and observed prey ingestion rates. Application of the best-performing model revealed strong seasonal patterns in prey ingestion rates in the Wadden Sea that varied between years.

Conclusions We show that prey ingestion rates of spoonbills can be fairly accurately estimated from acceleration data. These results are promising for the use of spoonbills equipped with GPS/ACC-trackers as monitors of spatial and temporal variation in the availability of small fish and shrimp, which is key to understand the foraging and migratory movements of spoonbills and provides information on the quality of (coastal) wetlands.

Keywords Biologging, Accelerometer, Machine learning, Foraging success, Waterbird, Bioindicator, *Platalea leucorodia*

[†]Tamar Lok and Matthijs van der Geest contributed equally to this work

*Correspondence:

Tamar Lok

tamarlok@gmail.com

Full list of author information is available at the end of the article



Background

Foraging is essential for animals to survive and successfully reproduce. Determining where animals forage and how successful they are is key to answering many ecological questions [1]. For example, this information is crucial to understand habitat use [2], foraging decisions [3–5], movement patterns [6] and time budgets [7]. In addition, quantifying (individual) variation in foraging success in space and time and in relation to age, sex and experience helps explain variation in reproductive performance [8–10] and survival and their consequences for population dynamics [11, 12]. Moreover, information on foraging habitat use and success can be used for nature conservation purposes, through identifying the importance and quality of foraging sites [13, 14].

While food intake rates of animals feeding on plants or sessile prey may be predicted from measuring the density, availability and quality of their food [15–17], this approach is less reliable for animals foraging on mobile prey. First, the distribution of mobile prey may change over short time scales and second, prey may behaviourally respond to sampling efforts. Therefore, to get reliable and accurate estimates of prey intake rates for predators foraging on mobile prey, direct visual observations are preferred. However, such visual observations are challenging or even impossible when species are difficult to approach, forage in vast or inaccessible areas, or at night. In these cases, the rapid development and miniaturization of tracking devices may provide a solution [18]. Tracking devices that simultaneously collect location and acceleration data allow the monitoring of not only the locations that animals are visiting, but also of what they are doing at these locations [19–21]. However, while machine learning techniques have been widely and successfully applied to distinguish behaviours such as walking, resting and flying [20], only a few studies succeeded to accurately distinguish behaviours associated with prey captures. In some species, the time from prey capture to swallowing is relatively short, allowing it to be detected as a whole (penguins [22, 23] and marine mammals [24, 25]). In other studies, rather than the actual capture, behaviours following a prey capture could be distinguished, such as prey handling, eating or caching [26–28].

That only few studies succeeded in distinguishing behaviours related to prey captures may be partly due to species-specific characteristics of the foraging behaviour (with only some species making distinct movements when catching, handling or swallowing (eating) prey), but also on how acceleration data are collected. For example, in most of the above-mentioned studies, where the actual prey captures could be distinguished [22–25], accelerometers were taped onto the head or mandibles, thereby

picking up subtle movements of the head or mouth, with the specific aim to detect prey captures. These taped accelerometers only stayed on the animals for a few days, hence the obtained information is limited to foraging grounds around the place where the animal can be recaptured to retrieve the trackers [29]. For longer term deployments, with the primary aim to collect long-term individual data on habitat use and daily and seasonal (migratory) movements over multiple years, trackers (often solar-powered) are usually attached onto a neck collar (terrestrial mammals [30] and some birds (geese and swans [31, 32]) or back-mounted harness (birds [33])). With such tracker placements, prey captures are likely harder to distinguish, while having this information would greatly aid the interpretation of observed movement patterns, and enable individual-level quantification of foraging success in space and time.

A species that does make a very distinct movement upon capturing a prey (to swallow it) is the Eurasian spoonbill *Platalea leucorodia* (hereafter spoonbill). Spoonbills are wading birds that feed tactically on small fish, shrimps and other crustaceans that live in the water column. They forage during both day and night and in waters of varying salinity, ranging from freshwater to marine [34]. The fact that their prey are mobile makes reliable sampling of prey distribution and availability difficult, if not impossible. Prey may behaviourally respond to sampling activities or attributes (e.g., nets), and their distribution and availability may change in relation to tide, the diurnal cycle and over the season. Moreover, spoonbills use vast areas for foraging, and visit many different wetlands during migration and in winter [35]. A better understanding of their migratory decisions and performance would require information about prey availability at all these wetlands, which is practically impossible to achieve through prey sampling. These issues could be (partly) solved if prey captures could be detected from tracked spoonbills. Spoonbills search for prey by walking through shallow water while making sweeping movements with their hypersensitive bill through the water [34]. When a prey is detected, they try to capture it between the flattened and broadened tips of their bill. Sometimes a short chase is needed before the prey is captured (presumably when the bird feeds on a shoal of fast-swimming fish). When a prey is successfully captured between the tips of their bill, spoonbills make a distinct movement with their head and neck to throw the prey into their throat to swallow it [36].

In this study, we investigate whether searching for and ingesting prey by spoonbills can be accurately distinguished from other behaviours on the basis of accelerometer data collected by trackers (hereafter referred

to as GPS/ACC-trackers) mounted on the back of the birds. For this, we collected data on the actual behaviour of 5 spoonbills equipped with a GPS/ACC-tracker by video-recording them in a variety of natural ecological contexts. Using these annotated data, we applied supervised machine learning techniques (using random forest models) and compared classification performance for nine behaviours using two segmentation techniques: fixed-time and flexible-time segmentation [27]. Flexible-time segmentation has been suggested to perform particularly well on distinguishing short-lasting behaviours [27]. However, its performance may depend on the length of the acceleration data samples. For the fixed-time segmentation method, segment length is expected to influence classification performance [37]: to distinguish short-lasting behaviours such as prey ingestions, short segment lengths of the same or shorter length than the natural duration of the behaviours are expected to perform best.

Selecting the best-performing classification model, we then applied it on acceleration data collected by the GPS/ACC-trackers of eight adult female spoonbills foraging in the Wadden Sea (The Netherlands) during the breeding seasons of 2016–2019 to explore how prey ingestion rates vary throughout the breeding season and between years. In the Wadden Sea, the diet of spoonbills in terms of biomass consists mostly of juvenile flatfish (mainly plaice, *Pleuronectes platessa*), gobies (*Pomatoschistus* spp.), three-spined sticklebacks (*Gasterosteus aculeatus*) and smelt (*Osmerus eperlanus*) [38, 39]. In terms of numbers, which is the relevant measure for comparison with prey ingestion rates, juvenile flatfish and brown shrimp *Crangon crangon* are most abundant in the diet [38, 39]. Studies on the seasonal presence of plaice [40, 41] and brown shrimp [42, 43] show an initial increase from April to June followed by a decrease. We explore whether this seasonal pattern is reflected in the prey ingestion rates of spoonbills foraging in the Wadden Sea. Finally, we discuss the implications of our results for spoonbills to be used as a bioindicator of (coastal) wetland habitat quality.

Methods

GPS tracking

Between 2012 and 2018, 32 adult spoonbills (21 males and 11 females, see Additional file 1: Table S1) were caught in the breeding colony on the Dutch Wadden Sea barrier island Schiermonnikoog (N 53.48°, E 6.25°) and equipped with a UvA-BiTS tracker [44]. These trackers measure GPS location along with a sample of 20 Hz tri-axial acceleration data and allow for flexible sampling settings [sampling interval and in case of acceleration data, sampling duration (1–10 s)] which can be remotely

adjusted via communication with radio antennas connected to a computer. The collected data are stored in the on-board memory (4–32 MB) of the tracker and downloaded when the bird is in reach of the antenna network that was set up in the breeding colony. Accelerometers were calibrated to convert the three components of the acceleration data in g-force ($1\text{ g} = 9.8\text{ m s}^{-2}$).

All birds were caught on the nest using a leg loop. A nylon thread (of c. 2 mm thickness) was placed in a large loop around the nest bowl, which then ran through a small loop to a person hiding at 20–30 m from the nest. When the bird had resumed incubating the eggs, the person pulled the thread, thereby closing the large loop around the leg of the bird. We selected individuals for catching that were strongly attached to the nest (i.e., not flying up when approached until c. 30 m from the nest). In the majority of cases, these birds were in the second half of incubation. During catching, the eggs were temporarily replaced by dummy eggs. In the few cases that a bird was not caught within half an hour, the catching attempt was aborted.

Upon capture, the bird was measured, weighed and a blood sample was taken for molecular sexing. The bird was ringed with a unique combination of colour-rings and a flag and a GPS/ACC-tracker was mounted on the back of the bird using a Teflon wing harness [33]. The tracker including the neoprene pad and Teflon harness (5 g) weighed 31 ± 12 g (mean \pm sd), and the body mass of the caught adult females and males was 1646 ± 146 g and 1968 ± 162 g, respectively. The tracker contributed 1.1–3.0% to the spoonbill's body mass (see Additional file 1: Table S1 for body mass and tracker weight per individual), thus not exceeding the 3% that has been suggested to represent the upper limit for migratory bird species [45]. After handling, which took maximally half an hour, the birds were released immediately.

Collection and behavioural annotation of video footage

The workflow from collecting acceleration data to developing and testing behavioural classification models is shown in Fig. 1. First, we collected video material of several GPS/ACC-tracked individuals. To this aim, we searched for the tracked individuals at their foraging grounds and in the colony in June 2013–2015 and August 2013–2014. Whenever a bird was encountered, the measurement scheme of the tracker was temporarily adjusted to the maximum sampling duration of 10 s of acceleration data and a sampling interval of 10 s, implying (nearly) continuous collection of acceleration data. We filmed the birds with a camera mounted on a 20–60 × spotting telescope.

We designed an ethogram of 13 different behaviours (Additional file 1: Table S2) and assigned these

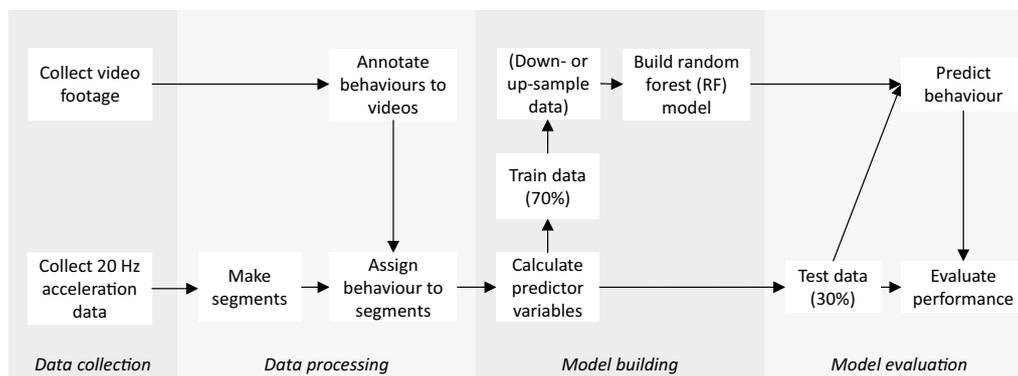


Fig. 1 Machine learning workflow for random forest classification of observed behaviours, adjusted after [27] and [60]

to acceleration data which were synchronised with the collected video material (see Additional file 2: Video S1). The video material contained very few data on passive (soaring/gliding) flight, as this type of flight mainly occurs during migration. Therefore, we graphically annotated additional data on passive (soaring or gliding) flight by examining plots of acceleration data samples collected during migratory flights of three individuals, during which spoonbills use both active (flapping) and passive flight. These two types of flight give very different acceleration patterns (Additional file 1: Figure S1, [46]).

In total, we annotated 1.6 h of video material of 5 birds. The total duration of video-annotated data of the different behaviours, as well as of the graphically annotated passive flight data, is shown in Additional file 1: Table S2. The duration during which behaviours were continuously expressed is shown in Additional file 1: Figure S2, as an upper limit to the desired length of the segments on which to apply the behavioural classification algorithm (i.e., segments should not be longer than the mean duration of a behaviour, otherwise segments are likely to consist of a mixture of different behaviours; for more details on the segmentation, see below). Figure 2 shows representative acceleration data patterns for the most relevant behaviours.

Segmentation, summary statistics and behaviour assignment

All calculations and analyses were performed in program R (version 3.6.0 [47]). We calculated summary statistics to characterize the acceleration data within segments of acceleration data and used them as predictor variables for machine learning. These segments can be of fixed length ('fixed segmentation') or of variable lengths ('flexible segmentation') for which an automated procedure is used to cut the acceleration data sample into smaller segments based on changes in the

acceleration data signal. The idea of the flexible segmentation method is that this would create segments that are likely to be cut at the point where a change in behaviour occurs, as reflected by a change in the acceleration data signal, and hence that flexibly cut segments (of variable length) are more likely to consist of a single behaviour than fixed-length segments. Indeed, the flexible segmentation method has previously been shown to result in higher accuracy of behavioural classification compared to the fixed segmentation method [27]. However, the sampling duration of acceleration data analysed in [27] was 10 s, while the trackers in our study collect much shorter acceleration data samples (of 0.8 or 1.6 s, see above). With such short samples, the flexible segmentation method may perform less well. Therefore, we compared the classification performance of the fixed versus flexible segmentation method using a sampling duration of maximally 1.6 s. These samples were then cut into segments of fixed length (of 0.2, 0.4, 0.8, or 1.6 s) or of variable lengths (between 0.15 and 1.6 s), for which we used a change-point model framework that cuts the samples into smaller segments based on changes in the x -signal (as in [27]), using the *processStream* function of the R package *cpm* [48]. We selected the GLR (Generalized Linear Ratio) test statistic to detect changes in both the mean and variance of the x -signal. The sensitivity of the change-point model to changes in the x -signal is determined by the ARL_0 (Average Run Length) parameter, which reflects the average number of observations before a false positive is detected. When ARL_0 increases, the probability of detecting a change-point decreases, resulting in on average longer segments. We compared model performance for different values of ARL_0 (100, 500, 5000 and 50,000). To each segment, we assigned the behaviour that was expressed during most of that segment. Additional file 1: Figure S3 and S4 show the distribution of segment lengths for the different ARL_0 values and per

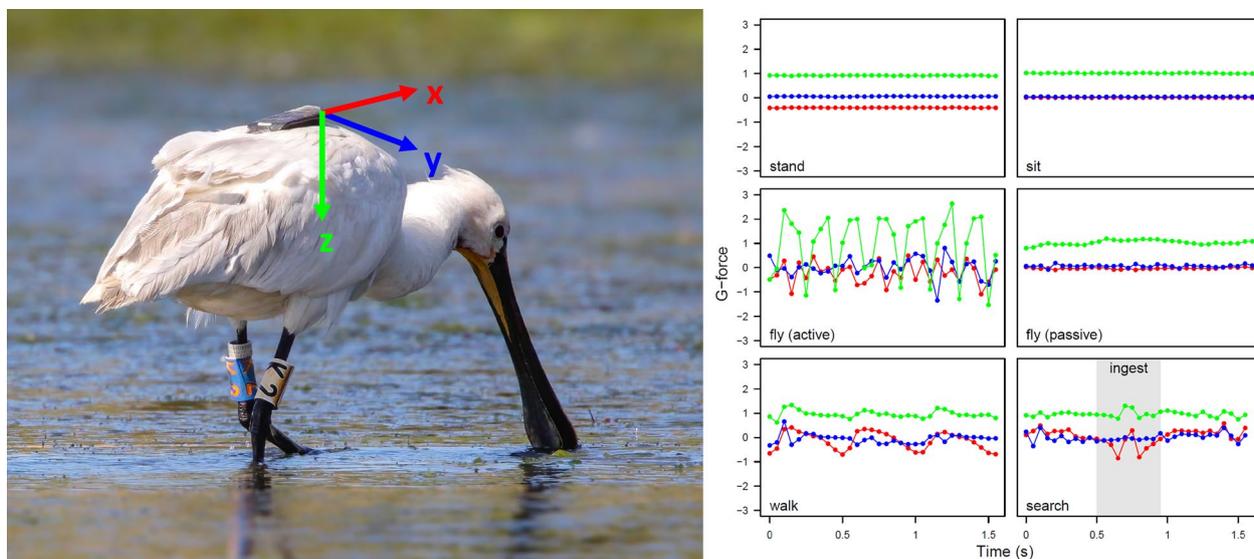


Fig. 2 Foraging spoonbill equipped with a GPS/ACC tracker along with representative acceleration data patterns. The arrows indicate the three directions in which acceleration is measured by the tracker. On the right panel, representative acceleration data patterns (at 20 Hz) for the most relevant behavioural classes, with the bottom right panel representing foraging behaviour, including both searching for and ingesting a prey (the shaded area). Photo credits: Vasco Valadares

assigned behaviour when the flexible segmentation method is applied to the annotated data set.

Per segment, the following summary statistics were calculated for each of the three axes (x, y and z): mean, maximum value, minimum value, skewness, kurtosis, dominant power spectrum, frequency at the dominant power spectrum (Hz), trend, noise and mean dynamic body acceleration. In addition, overall dynamic body acceleration (ODBA) was calculated as the sum of the mean dynamic body acceleration over each axis [49]. We also used GPS speed as a predictor variable, as measured by the GPS device along with the acceleration sample. Skewness and kurtosis reflect the extent to which the distribution of values is left- or right-skewed and the height of the distribution and were calculated using the R package *moments* [50].

Machine learning classification algorithm

We used random forest (RF) models to predict behaviour from acceleration data, as these models have been shown to perform consistently well [6, 27, 51, 52]. RF models were run using the R package *randomForest* [53]. Using a resampling procedure, we randomly split the annotated data into a train and test data set: 70% of the data were used to train the model. Its performance in correctly predicting the different behaviours was then tested on the remaining 30% of the data. To derive mean and 95% confidence intervals for the classification performance

measures of the model (see below), this procedure was repeated 100 times.

To estimate the classification performance of the RF model per behavioural class, each classified segment was labelled as either positive (classified as this behaviour) or negative (classified as a different behaviour) and as either correctly (true) or incorrectly (false) classified, resulting in four categories: true positive (TP), true negative (TN), false positive (FP) and false negative (FN). These statistics were then used to calculate precision ($\frac{TP}{TP+FP}$), reflecting the proportion of positive classifications that were correct, and sensitivity ($\frac{TP}{TP+FN}$), reflecting the probability that a given behavior is classified as such. In addition, we calculated the F-measure ($\frac{2TP}{2TP+FP+FN}$) which is the harmonic mean of precision and sensitivity [54].

Using segments of 0.4 s, we first explored whether classification performance (F-measure) was improved by down- versus up-sampling the amount of annotated data (by deleting versus repeating part of the segments) of behaviours that occurred relatively often (stand, search) versus infrequently (drink, walk, fly-passive, handle, ingest) to achieve a more balanced data set to train the RF models. We also explored whether classification performance improved when using only the most important predictor variables in the RF models instead of all predictor variables. These procedures hardly improved the classification performance (F-measures) of the different behaviours (Additional file 1: Figure S5). However,

as down-sampling the amount of annotated standing behaviour did not decrease model performance, but significantly decreased computational time, we nevertheless down-sampled the number of annotated acceleration segments in which the most often expressed behaviour was “stand” by a factor 4. We then compared the classification performance for the different behaviours using either the fixed-time or the flexible-time approach, with different segment lengths and ARL_0 -values, respectively.

Application: seasonal and annual variation in prey ingestion rates

We selected the segmentation method (with associated segment length or ARL_0 value) that resulted in the highest F-measures of the RF-model, in particular for behaviours associated with foraging (searching, handling and ingesting prey). We applied this method to acceleration data collected by 8 adult spoonbills breeding on Schiermonnikoog in the period 2016–2019 (Additional file 1: Table S3), with the aim to investigate whether we could detect seasonal and annual variation in prey ingestion rates from acceleration data. During this period, all trackers were set to collect a GPS location along with 1.6 s of acceleration data every 10 min. To reduce variation due to habitat-specific prey composition and densities, and because most foraging (both in the annotated and application data set) occurred in the Wadden Sea, we only used data from the Wadden Sea for this proof-of-concept analysis. To select data from the Wadden Sea, we overlaid the GPS positions collected together with the acceleration data samples with the tidal basin map of Baptist et al. [55]. In addition, to reduce variation due to sex-specific habitat or prey preferences, with females foraging almost exclusively in the Wadden Sea, while males spend about 50% of their foraging time in freshwater habitats (Lok et al. in prep), we only selected data from females.

From the classified data, we calculated prey ingestion rate (min^{-1}) per bird per date by dividing the time spent ingesting prey (sum of duration of segments classified as “ingest prey”) by the time spent foraging (i.e., the sum of the duration of segments classified as “search”, “handle” or “ingest prey”). This proportion was then divided by the average duration of a prey ingestion (0.8 s, Additional file 1: Figure S2) and multiplied by 60 s to get the number of prey ingested per minute.

To model prey ingestion rates, we used linear mixed effects models [56] using R package *nlme* [57]. As data were positively skewed, prey ingestion rates were log-transformed. To investigate statistical support for variation in prey ingestion rates throughout the breeding season, we compared models with and without a linear

or quadratic effect of day of the year. We also explored whether there was support for annual variation in prey ingestion rates, and for differences in seasonal patterns between years by considering models with year as categorical variable and models with an interaction between year and (the linear or quadratic effect of) day of year. We accounted for pseudoreplication and individual variation in prey ingestion rates by modelling random individual variation around the intercept and (where applicable) slope parameters describing the seasonal pattern. In the statistical analyses, we only used prey ingestion rates that were calculated from at least 20 s of acceleration data classified as foraging per individual per day. Candidate models were run using maximum likelihood estimation and their relative support was evaluated based on the Akaike Information Criterion, corrected for small sample size (AIC_c [58, 59]). We selected the most parsimonious model as the best description of the data, being the model with the fewest parameters among the supported models (with $\Delta AIC_c < 2$).

The R code to run the analyses has been made available at Github.

Results

Classification performance in relation to segmentation method and segment length

Irrespective of segmentation method or segment length, sensitivity and precision were very high (0.94–1.00) for inactive behaviours (sitting and standing) and active (flapping) and passive (soaring/gliding) flight (Fig. 3). In contrast, sensitivity was very low for prey handling (< 0.1) and drinking (< 0.2). Precision, and hence the F-measure, could not be calculated for these behaviours, as they were not predicted in the test data set in any simulation. Sensitivity and precision for walking, searching and ingesting prey varied between 0.5 and 0.9 and depended on segment length (fixed-time segmentation) or ARL_0 value (flexible time-segmentation, Fig. 3).

For walking, both sensitivity and precision, and therefore, the F-measure, initially increased with segment length to stabilize at segment lengths of 0.6–2.0 s. For searching, sensitivity slightly decreased with increasing segment length, to increase again at 2.0 s, while precision was highest at intermediate segment lengths (0.4–1.0 s). As a result, the F-measure for searching was highest at segment lengths of 0.4–0.6 s (mean: 0.91, 95% CI: 0.90–0.92). For ingesting prey, sensitivity initially increased with segment length to become more or less stable between 0.4 and 1.0 s to rapidly decrease when segments were > 1.0 s, while precision was highest at 0.4 s and then gradually decreased with increasing segment length. As a result, the F-measure for ingesting prey was highest at

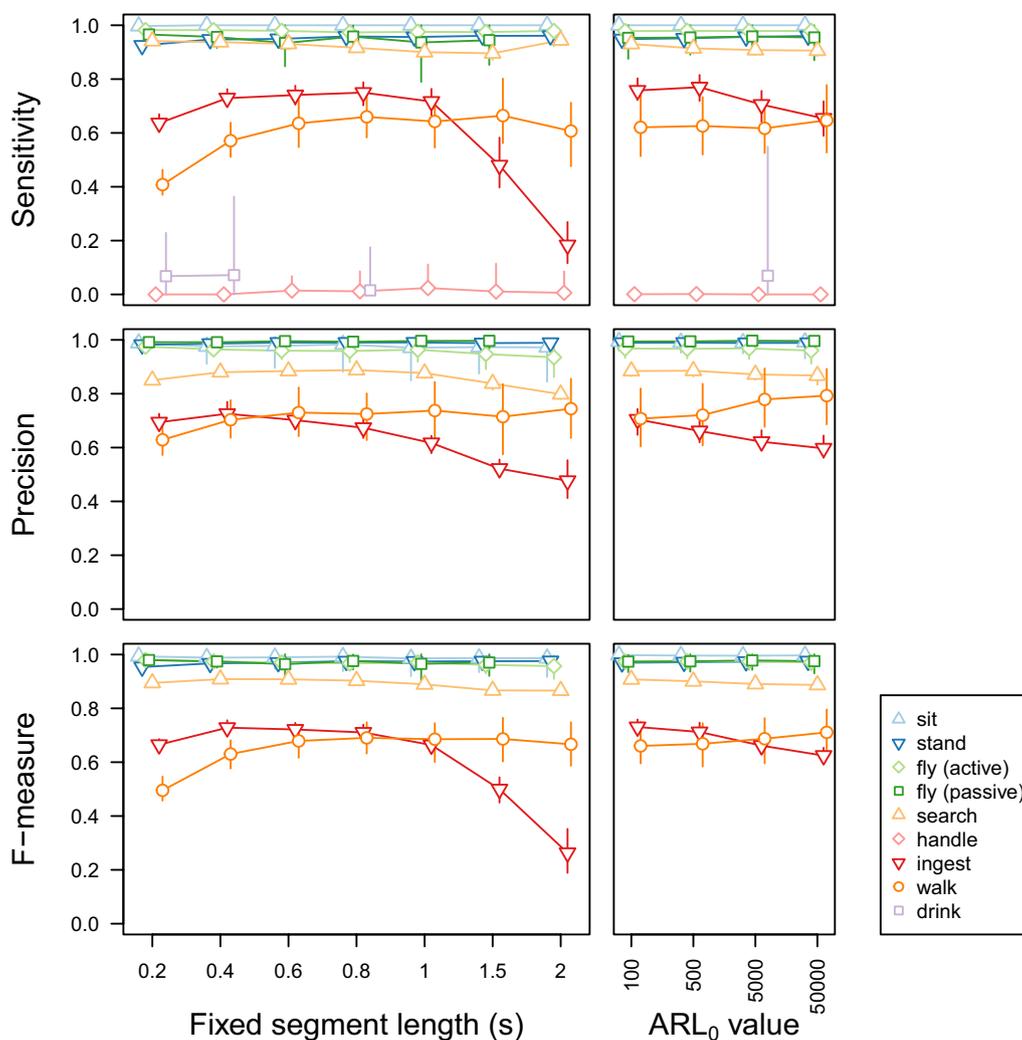


Fig. 3 Classification performance (mean and 95% confidence interval) of the random forest model as a function of fixed segment length (left panel) and of ARL_0 for the flexible segmentation method (right panel). To derive 95% confidence intervals, the model training and testing procedure was repeated 100 times on different randomly selected 70% train and 30% test data sets. Note that for passive flight, no segments of 2 s were available, hence classification performance for this segment length could not be determined

0.4 s (0.73, 0.70–0.76). Using the flexible segmentation method, sensitivity and precision decreased with increasing ARL_0 value for ingesting prey and, to a lesser extent, for searching. In contrast, precision and the F-measure for walking were slightly higher (though CRI’s overlap) at higher ARL_0 values. The highest F-measures for searching (0.91, 0.90–0.92) and ingesting prey (0.73, 0.70–0.77) were obtained with $ARL_0=100$ (Fig. 3). The amount of annotated data of drinking and handling prey was too small to draw robust conclusions.

Ingesting prey was most often confused with searching, as was the case for walking, with false positive and false negative confusions with searching occurring similarly often (Additional file 1: Figure S6). Consequently,

the estimated prey ingestion rates closely matched the observed prey ingestion rates (Table 1).

Application of the best-performing model to estimate prey ingestion rates

The F-measures for searching and ingesting prey were highest using either the fixed-time segmentation method with a segment length of 0.4 s or the flexible-time segmentation method with an ARL_0 -value of 100 (Fig. 3). We applied both methods to analyse the acceleration data from 8 adult female spoonbills in the Wadden Sea. Here, we show the results from the fixed segmentation method with a segment length of 0.4 s. Results from the flexible-time segmentation model with $ARL_0=100$ can be found

Table 1 Deviation of predicted prey ingestion rates from the observed using the different segmentation methods and different segment lengths and ARL_0 -values. In most cases, the confidence intervals (estimated from 100 simulations) include 1.0 (no deviation), indicating that both methods predict prey ingestion rates that are very close to the true value

Segmentation method	Parameter value	Deviation of predicted from observed prey ingestion rate
FIXED	Segment length (s)	
	0.2	0.87 (0.81–0.91)
	0.4	0.97 (0.90–1.04)
	0.6	1.02 (0.96–1.10)
	0.8	1.08 (0.99–1.17)
	1.0	1.12 (1.03–1.20)
	1.6	0.89 (0.74–1.10)
FLEXIBLE	ARL_0 value	
	100	1.03 (0.95–1.13)
	500	1.12 (1.00–1.22)
	5000	1.09 (0.97–1.19)
	50,000	1.06 (0.91–1.18)

in the supplementary material (Additional file 1: Figure S7).

The distribution of the locations in the Wadden Sea where the birds were classified to have been foraging are shown in Fig. 4. The best-supported model describing

seasonal and annual variation in prey ingestion rates at these locations included a statistical interaction between season (described by a quadratic function of day of the year) and year (with $\Delta AIC_c = 28.35$ compared to the second model which included additive effects of season and year, Table 2). Prey ingestion rates more than doubled from early April to late June to decrease again toward the end of September (Fig. 5a). The seasonal pattern differed between years, with prey ingestion rates peaking about 2 weeks later (around 5 July) in 2016 compared to 2017–2019 (around 21 June, Fig. 5b). Moreover, prey ingestion rates at the seasonal peak were about 5% lower in 2016–2017 compared to 2018–2019.

With the flexible segmentation method, similar seasonal patterns were found, but prey ingestion rates were estimated consistently (on average 33%) lower than with the fixed segmentation method (Additional file 1: Figure S7).

Discussion

The aim of this study was to assess how well searching for and ingesting prey, among other behaviours, could be distinguished from acceleration data collected by tracking devices permanently mounted on the back of Eurasian spoonbills, to estimate prey ingestion rates. We show that ingesting prey could be fairly accurately (F-measure: 0.73) classified from acceleration data, using either short fixed-time (of 0.4–0.8 s) or flexible-time segmentation. Most longer-lasting behaviours, including resting,

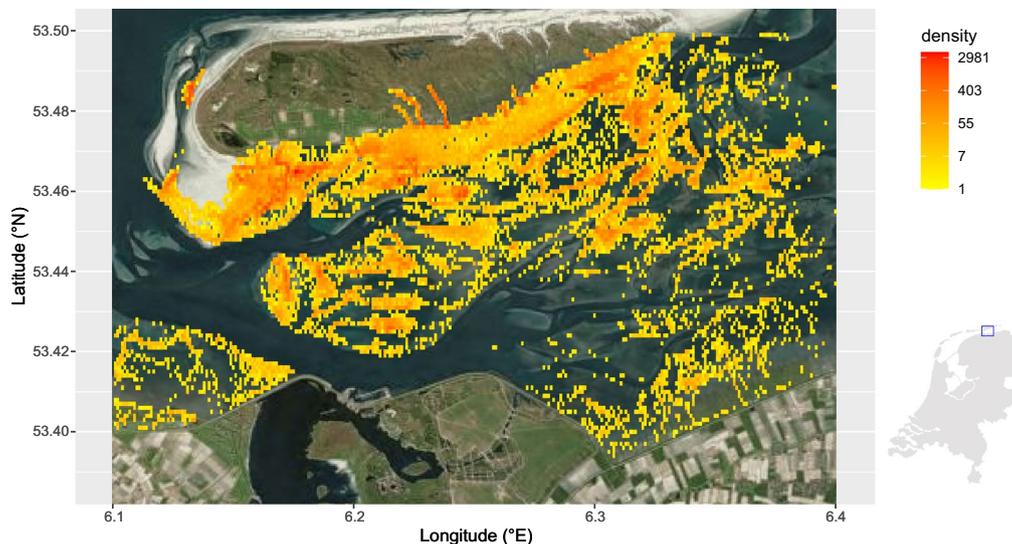


Fig. 4 Spatial distribution of foraging locations of adult female spoonbills in the Wadden Sea south of their breeding colonies on Schiermonnikoog. Data are pooled across individuals ($N=8$), months (March–October) and years (2016–2019). Locations are here defined as latitude and longitude rounded to the third decimal. To improve readability, the density, reflecting the total number of 0.4 s segments of acceleration data estimated as foraging at each location across all individuals, is plotted on a log-scale. The location of the plotted area within The Netherlands is shown in the bottom right

Table 2 Model selection of seasonal and annual variation in prey ingestion rates, estimated by the RF model applied to 0.4 s segments of 20 Hz acceleration data

	df	ΔAIC_c	Akaike weight
season * year	19	0	1.00
season + year	13	28.35	0.00
season	10	53.84	0.00
year	6	1191.11	0.00
–	3	1206.01	0.00

Season is modelled as a quadratic effect of day of the year (yday): $\beta_0 + \beta_1 \cdot \text{yday} + \beta_2 \cdot \text{yday}^2$. For the model season * year, the three β -parameters are estimated separately for each year. All models include a random intercept (random variation around β_0), and for the models with seasonal effects also random slopes (random variation around β_1 and β_2), with individual as random effect

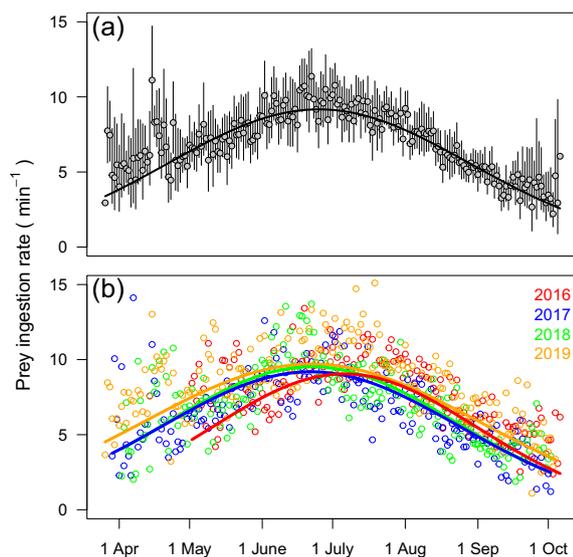


Fig. 5 Seasonal pattern and annual variation in prey ingestion rates of spoonbills foraging in the Wadden Sea. Results are based on 8 adult females that were tracked during the period 2016–2019 (for more details on the available data, see Table S3). The trackers collected 1.6 s acceleration data samples along with GPS coordinates at 10 min intervals. For training and applying the RF model, the data were cut into 0.4 s segments. **a** The line reflects the population-level estimates from the mixed-effect model fitting a quadratic function of day of the year while accounting for random individual variation in the intercept and linear and quadratic effect of day of the year (based on the 3rd ranked model “season” in Table 2). **b** Means and estimated seasonal trends are plotted separately for each year (based on the best-supported model “season * year” in Table 2). Means and 95% confidence intervals were calculated from the estimates of prey ingestion rates (i.e., proportion of foraging time spent ingesting prey) per bird per year per day of the year on the log scale and then back-transformed. For readability, 95% confidence intervals are only shown in panel **a**

flying and searching (for food), were accurately classified (F-measures: 0.85–0.94) over a large range of fixed-time segment lengths as well as with the flexible-time segmentation. Application of the RF model on 0.4 s segments of acceleration data collected between 2016 and 2019 on 8 female adult spoonbills foraging in the Wadden Sea during the breeding season revealed that the classification accuracy of relevant foraging behaviours, including ingesting prey, was sufficiently high to detect seasonal and annual variation in prey ingestion rates. While several previous studies on diving birds and mammals showed that prey ingestions could be distinguished from data collected by accelerometers mounted on their head or mandibles [22–25], this study is among the first to quantify prey ingestion rates for a long-distance migratory bird equipped with a back-mounted GPS/ACC-tracker. Although the classification accuracy of ingesting prey in our study was somewhat lower than in the studies on diving animals (with reported sensitivity, precision, specificity and/or overall accuracy between 0.81 and 0.91), the estimated prey ingestion rates in our study closely matched reality (Table 1). As the solar-powered trackers stay on the birds for the rest of their life and usually function for several years (up to 8 years, pers. obs.), this allows for long-term monitoring of prey ingestion rates at high resolution across time and space.

Methodological considerations

Handling prey was very poorly classified, and in most cases confused with ingesting prey (Additional file 1: Figure S6). This could be explained by the fact that the few cases of handling in the annotated data set (40 s of handling compared to 471 s of ingesting prey, Additional file 1: Table S2) often concerned unsuccessful attempts to throw the prey from the tip of the bill into the throat, which gives a very similar pattern in the acceleration data as when this throwing movement was successful (i.e., defined as ingesting prey). As handling occurred rarely, it only had a minor effect on the precision of classifying ingesting prey. Besides handling, drinking was poorly classified, presumably because it occurred only rarely in the annotated data set (Additional file 1: Table S2). Drinking was most often confused with standing (Additional file 1: Figure S6), which makes sense because spoonbills stand still when they drink. Combined with the fact that drinking is a rarely occurring behaviour of spoonbills in general, we suggest to pool it with standing.

The strong decrease in sensitivity of ingesting prey at fixed-time segments of > 1.0 s (Fig. 3) could be explained by the fact that these segments are longer than the

average duration of a prey ingestion (0.8 s, Additional file 1: Figure S2), and, therefore, often consist of a mixture of different behaviours, thereby giving a less distinct “prey ingestion” signal. However, an alternative explanation could be that—for the same reason—the sample size of annotated segments, where ingesting prey was the most occurring behaviour decreased relatively faster compared to other behaviours with increasing segment length. To remove this potential statistical artifact, we redid the analysis with the sample size that was available per behaviour when the data were split into 2.0 s segments (i.e. the smallest sample size) for all segment lengths, which produced similar results (Additional file 1: Figure S8).

When applied to the data of foraging adult female spoonbills in the Wadden Sea, the fixed-time segmentation method estimated consistently higher prey ingestion rates than the flexible-time segmentation method (Additional file 1: Figure S7). This seemingly contradicts the results from the annotated data set, where the two methods estimated similar prey ingestion rates that were close to the observed (Table 1). As the application data set is much larger (169 h) than the annotated data set (1.6 h), we consider the results from the application data set more reliable. The difference in estimated prey ingestion rates by the two methods was mainly driven by a difference in the estimated proportion of time spent ingesting prey rather than the time spent searching (Additional file 1: Figure S9). One possible explanation for this is that the change-point model used in the flexible segmentation method misses prey ingestions that are detected when the sample is cut into small fixed-time segments, and, therefore, underestimates the time spent ingesting prey. On the other hand, the fixed-time segmentation may overestimate the time spent ingesting prey as parts of one prey ingestion may end up in different segments, with potentially only a small part of a prey ingestion needed to classify this segment as ingesting prey. For the translation into energy intake rates (see below), it is important to know which method most closely resembles the actual prey ingestion rates, but for quantifying (relative) differences between individuals or in time and space, both methods are suitable, as indicated by the similar seasonal pattern detected with both methods. The overall estimated time budgets by the two methods is shown in Additional file 1: Figure S10.

In our study, we used a sampling frequency of 20 Hz, because this was the frequency at which the acceleration data of our tagged spoonbills were collected and we expected that such a high frequency was needed to achieve the highest classification performance of short-lasting behaviours such as ingesting prey. However, when the primary goal is not to estimate prey ingestion

rates but to distinguish broader behavioural categories, sampling frequency may be reduced to save memory and battery power (to transmit the data), as other studies showed that a variety of behaviours can already be accurately classified at sampling frequencies of 5 Hz [60]. Indeed, down-sampling from 20 to 2 Hz (to still be able to calculate and use standard deviation as a predictor variable with a segment length of 0.8 s) revealed that inactive behaviours (stand, sit) and some active behaviours (fly-active, fly-passive and search) are already well-distinguished at the very low sampling frequency of 2 Hz (F-measures ≥ 0.82 , Additional file 1: Figure S11). In contrast, the F-measure for walking and ingesting prey strongly increased with sampling frequency, suggesting that classification performance may be improved when using sampling frequencies > 20 Hz (Additional file 1: Figure S11). When pooling the behaviours walking, searching, handling, drinking and ingesting prey into a single category (“active on the ground”), the pooled behavioural categories (resting, active on the ground, active flight and passive flight) all have F-measures ≥ 0.90 , even at 2 Hz.

Biological considerations

The estimated prey ingestion rates of 8 adult female spoonbills foraging in the Wadden Sea initially increased from April onward to reach a maximum in June, after which they gradually decreased until September when the birds departed on autumn migration (Fig. 5). This seasonal pattern qualitatively coincides with published data on the seasonal presence of several important prey species of spoonbills in the Dutch Wadden Sea [38], including juvenile flatfish [40, 61] and brown shrimp [42, 43]. This suggests that the estimated prey ingestion rates are indicative of prey densities, with the initial increase likely driven by settlement of juvenile flatfish and the spawning of brown shrimp in the Wadden Sea. The subsequent decrease in prey ingestion rates may be caused by a decrease in prey densities due to predation and other sources of mortality, and of growing prey moving to deeper waters [62].

Prey ingestion rates reflect the number of prey ingested per unit time. To make the translation from prey ingestion to energy intake rate, (1) estimated prey ingestion rates should reflect actual prey ingestion rates and (2) additional information is required on prey sizes, species composition and associated energy content and how these change throughout the breeding season. Such information could, for example, be obtained from diet analysis of droppings and/or regurgitates throughout the breeding season to estimate changes in the proportion of different prey species and their size distribution (see [38]). Nonetheless, the period with the highest prey

ingestion rates closely matches with the period that most spoonbills on Schiermonnikoog have chicks in the nest, as the average hatch date is 11 May (measured during 2006–2009, [63]) and chicks fully depend on their parents for food during the following 6–8 weeks [34].

Our study focussed on the eastern Dutch Wadden Sea, where spoonbills mostly forage on small fish (mainly bottom-dwelling juvenile flatfish and gobies) and shrimp, which they search for by slowly wading through the water while sweeping their bill from side to side and, upon capture, usually ingest in a smooth continuous movement without involving any distinct handling (Additional file 2: Video S1). In other habitats, however, spoonbills may forage on different prey types and sizes which may require slightly different foraging techniques. For example, to catch pelagic fish, spoonbills have been observed to run through the water [36]. Moreover, handling time as well as the movements made during handling vary according to prey type and size, with larger prey generally involving longer handling to position the prey well between the bill tips, which usually happens underwater, and to transport the prey from the bill tips to the throat [36]. Therefore, additional video-annotated acceleration data on spoonbills foraging in different habitats and on different prey types and sizes is needed to verify the accuracy of prey ingestion rates across foraging habitats and to investigate whether handling and ingesting different prey types and sizes can be distinguished from accelerometer data [64, 65], potentially requiring sampling frequencies > 20 Hz, with the ultimate aim to be able to translate prey ingestion rates into energy intake rates throughout the annual cycle.

Conclusions

Our study showed that prey ingestion rates of individual spoonbills can be estimated from accelerometers mounted on the back of the birds. When combined with information on diet composition in terms of prey species and sizes (e.g., through sampling diets or further refinement of acceleration data analysis), the translation to energy intake rates can be made. This provides exciting opportunities to investigate the ecological consequences of temporal and spatial variation in energy intake rates, both at the individual and population level. At the individual level, it allows us to investigate how foraging success improves with age and how foraging and migratory decisions and (ultimately) fitness are influenced by the energy intake rates individuals experience throughout the annual cycle. At the population level, the possibility to quantify temporal and spatial variation in energy intake rates throughout the annual cycle will help us to better understand the seasonal timing of events (e.g., breeding, migration) and to explain temporal and spatial variation

in reproductive output and survival, and hence, population dynamics. Moreover, it allows GPS/ACC-tracked spoonbills to be used as an indicator of the availability of small fish and shrimp, and with that, as a bioindicator of the habitat quality of (coastal) wetlands.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-022-00315-w>.

Additional file 1: Figure S1. To improve the classification of passive (soaring/gliding) flight, we graphically inspected the acceleration data during autumn migration flights of three individuals (6283, 6287 and 6291). Here, the migratory flight of spoonbill 6291 on 25 September 2016, crossing Brittany (between the red bars) and then following the Atlantic coast of France (left panel), and the associated acceleration segments during the crossing of Brittany (right panel) are plotted. The light blue dots on the itinerary reflect the positions during which the bird performed passive flight based on visual inspection of the plotted acceleration segments on the right. We only selected samples that consisted entirely of passive flight, which are outlined in bold in the right panel. **Figure S2.** Duration of behaviours expressed during continuous sampling bouts of 10 s, which is a subset of all annotated data as shown in Table S2 for (a) all unique behaviours as distinguished during the video annotation and (b) pooled behaviours as described in Table S2. Sample sizes indicated on top reflect the number of times a behaviour was expressed for a certain amount of time, summed over the five observed birds. **Figure S3.** Distribution of segment lengths resulting from applying the flexible segmentation method to the annotated data set with different values for the ARL_0 parameter. Prior to applying the flexible segmentation method, the annotated data set was cut into samples of 1.6 s. The minimum number of measurements in a segment was set at 3 (i.e., 0.15 s for 20 Hz data). **Figure S4.** Distribution of segment lengths per assigned behaviour (i.e., the behaviour occurring during most of that segment) resulting from applying the flexible segmentation method to the annotated data set with $ARL_0 = 100$. Prior to applying the flexible segmentation method, the annotated data set was cut into samples of 1.6 s. The minimum number of measurements in a segment was set at 3 (i.e., 0.15 s for 20 Hz data). **Figure S5.** Explorative analysis of the effects of reducing the number of predictor variables and of down- and up-sampling the amount of annotated data used to train the random forest model for certain behaviours that were over- versus underrepresented in the data (search and stand versus drink, handle, walk and fly-passive). Down-sampling was done on the entire data set (to maintain the 70% train and 30% test data set), while up-sampling was only performed on the training data set (as identical (copied) segments would otherwise appear in the training and testing data set). The full predictor set contains 32 predictor variables, whereas the reduced predictor set uses only the predictor variables that were estimated to result in > 20% decrease in overall accuracy when removed from the model, as calculated by the function *importance* of the *randomForest* R-package. **Figure S6.** Proportion of observed behaviours classified as a certain behaviour (top row) and the proportion of predicted behaviours that were actually a certain observed behaviour (bottom row). **Figure S7.** Seasonal variation in prey ingestion rates of adult female spoonbills foraging in the Wadden Sea, as estimated by the fixed segmentation method with segments of 0.4 s (in blue) and the flexible segmentation method using $ARL_0 = 100$ (in orange). Although 95% confidence intervals are mostly overlapping, the flexible segmentation method estimates consistently—on average 33%—lower prey ingestion rates than the fixed segmentation method. **Figure S8.** Patterns of sensitivity, precision and F-measure when reducing the number of segments to the number of 2.0 s segments available for each behaviour (i.e. the smallest sample size). By doing so, we remove the potential effect of smaller samples sizes at longer segment lengths on classification performance. While this reduced the sensitivity and precision of particularly ingesting prey, the patterns in relation to segment length remained similar to those reported in Fig. 3 of the main paper. **Figure**

S9. Estimated percentage of time spent searching and ingesting prey by adult female spoonbills, overall (left panels) and when in the Wadden Sea (right panels), and the resulting prey ingestion rates when using the fixed segmentation method with segments of 0.4 s (in blue) and the flexible segmentation method using $ARL_0 = 100$ (in orange). From these graphs, it becomes clear that the lower estimated prey ingestion rates by the flexible segmentation method are mainly driven by the lower estimated proportion of time spent ingesting prey. Another remarkable difference is that the flexible segmentation method estimates a higher proportion of searching than the fixed segmentation method, but only early in the breeding season (i.e. in the months April–May) when the birds are attached to the nest for a considerable part of their time. This suggests that the flexible segmentation method performs worse in distinguishing incubating (sitting on the nest) from searching than the fixed segmentation method (see also Figure S10) and may as such overestimate the proportion of time spent searching, resulting in an underestimation of prey ingestion rates. **Figure S10.** Proportion of time performing different behaviours throughout the season. Adult females are known to spend about 50% of their time sitting on the nest during the incubation and early chick rearing phase (April–June). This graph thus shows that sitting is rather poorly distinguished from standing, as the birds were estimated to be sitting maximally 10% of the time. It is thus advised to pool sitting and standing into a single “inactive” category and use additional information to determine whether the bird was incubating (e.g., using the location of the nest). **Figure S11.** Classification performance as a function of acceleration sampling frequency (number of acceleration measurements per second) using a fixed segment length of 0.8 s. Segments of 0.8 s were used to still have two measurements in the sample with a sampling frequency of 2 Hz (which is needed to estimate ODBA, an important predictor variable). **Table S1.** Information on captured and tracked adult Eurasian spoonbills in the colony on Schiermonnikoog. Note that one individual (with colourcode LaG/RBYf) was caught three times (in different years) to replace its malfunctioning tracker. **Table S2.** Amount of annotated acceleration data (in seconds) per behavioural class recorded per bird (with the sex indicated in brackets) and in total. Note that for 6283, 6287 and 6291, passive flight data were graphically validated (based on visual inspection of acceleration graphs) instead of based on visual observation of the bird (see Fig. S1). Foraging behaviour was video-recorded for three birds at three different sites: 760 in the Wadden Sea (marine, N53.477° E6.284°), 763 in the Lauwersmeer (freshwater, N53.358° E6.256°) and 1608 in the Bantpolder (freshwater, N53.405° E6.151°). **Table S3.** Number of days per bird per month included in the analysis (i.e., with at least 20 s of acceleration data classified as foraging in the Wadden Sea) of seasonal variation in prey ingestion rates of adult female spoonbills foraging in the Wadden Sea.

Additional file 2: Video S1. Short video of bird 760 searching for and ingesting prey along with the associated acceleration data.

Acknowledgements

We thank Natuurmonumenten for permission to work in national park Schiermonnikoog, Yvonne Verkuil for molecularly sexing and Folkert Abma, Jose Alves, Cynthia Borrás, Marnix Bosma, Inge Bouten, Eddie Douwma, Camilla Dreef, Marycha Franken, Wilma Hendrikse, Silke Hooijmeijer, Wilko Kootstra, Philip Kramer, Iris Kromhout van der Lely, Clazina Kwakernaak, Marjolein Leenknecht, Helen MacArthur, Hacen Mohamed El Hacen, Annelies Olf, Remco Rood, Rinus van der Molen, Arne van Eerden, Oscar Verhoeven, Yvonne Verkuil, Connie Vermazen, Lida Wessels and Carl Zuhorn for their help in the field. We thank four anonymous reviewers for their comments that helped improving the manuscript.

Author contributions

TP, WB, MvdG and TL conceived and initiated this study; TP, PdG and TL caught the birds and deployed the GPS/ACC-trackers; PdG, WB, MvdG and TL managed the radio antenna system and GPS/ACC-tracker settings; MvdG and RB collected video footage of tracked spoonbills which MvdG used to annotate the associated acceleration data. TL analysed the data with support from RB, MvdG and WB; TL and MvdG wrote the manuscript; all authors contributed critically to the drafts and gave final approval for publication. All authors read and approved the final manuscript.

Funding

This research was financially supported by the Metawad project awarded to TP by Waddenfonds (WF209925), the Spinoza Premium 2014 awarded to TP and a Veni grant awarded to TL (016.Veni.192.245) by the Netherlands Organisation for Scientific Research. UvA–BiTS studies are facilitated by infrastructures for e-Ecology, developed with support of NLeSC and LifeWatch and carried out on the Dutch national e-infrastructure with the support of SURF Cooperative.

Availability of data and materials

Data and R-scripts associated with this manuscript are publicly available at the NIOZ Data Archive System (DAS) (<https://doi.org/10.25850/nioz/7b.byd>) and Zenodo (<https://doi.org/10.5281/zenodo.7541131>).

Declarations

Ethics approval and consent to participate

This research involved the catching, tagging (with rings and tracker) and sampling (of blood) of adult Eurasian spoonbills. These procedures were conducted under license numbers D6548 and AVD105002016446 following the Dutch Animal Welfare Act, and followed the ethical standards of the Dutch Centre for Avian Migration & Demography.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands. ²Wageningen Marine Research, Wageningen University & Research, P.O. Box 57, 1780 AB Den Helder, The Netherlands. ³Rudi Drent Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands. ⁴Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands.

Received: 14 September 2022 Accepted: 23 December 2022

Published online: 01 February 2023

References

- Stephens DW, Brown JS, Ydenberg RC. Foraging: behaviour and ecology. Chicago: University of Chicago Press; 2007.
- Piersma T. What is habitat quality? Dissecting a research portfolio on shorebirds. In: Fuller RJ, editor. Birds and Habitat: relationships in changing landscapes. Cambridge: Cambridge University Press; 2012. p. 383–407.
- Watanabe YY, Ito M, Takahashi A. Testing optimal foraging theory in a penguin–krill system. *Proc Royal Soc B: Biol Sci.* 2014;281:20132376.
- van Gils JA, Spaans B, Dekinga A, Piersma T. Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology.* 2006;87:1189–202.
- Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Pelt TIV, Kettle AB, Speckman SG. Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology.* 2007;88:2024–33.
- Nathan R, Spiegel O, Fortmann-Roe S, Harel R, Wikelski M, Getz WM. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J Exp Biol.* 2012;215:986–96.
- Wolf LL, Hainsworth FR, Gill FB. Foraging efficiencies and time budgets in nectar-feeding birds. *Ecology.* 1975;56:117–28.
- Cox SL, Authier M, Orgeret F, Weimerskirch H, Guinet C. High mortality rates in a juvenile free-ranging marine predator and links to dive and forage ability. *Ecol Evol.* 2019. <https://doi.org/10.1002/ece3.5905>.
- Blanckenhorn WV. Fitness consequences of foraging success in water striders (*Gerris remigis*; *Heteroptera*: *Gerridae*). *Behav Ecol.* 1991;2:46–55.

10. Annett CA, Pierotti R. Long-term reproductive output in Western Gulls: Consequences of alternate tactics in diet choice. *Ecology*. 1999;80:288–97.
11. Oro D, Cam E, Pradel R, Martinez-Abraín A. Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proc Royal Soc Lond Ser B-Biol Sci*. 2004;271:387–96.
12. Kraan C, van Gils JA, Spaans B, Dekinga A, Bijleveld AI, van Roomen M, Kleefstra R, Piersma T. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *J Anim Ecol*. 2009;78:1259–68.
13. Soanes LM, Bright JA, Angel LP, Arnould JPY, Bolton M, Berlincourt M, Lascelles B, Owen E, Simon-Bouhet B, Green JA. Defining marine important bird areas: testing the foraging radius approach. *Biol Cons*. 2016;196:69–79.
14. Chimienti M, Cornulier T, Owen E, Bolton M, Davies IM, Travis JMJ, Scott BE. Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behavior. *Ecol Evol*. 2017;7:10252–65.
15. van Gils JA, Dekinga A, Spaans B, Vahl WK, Piersma T. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. *J Anim Ecol*. 2005;74:120–30.
16. Stillman RA, Wood KA, Gilkerson W, Elkinton E, Black JM, Ward DH, Petrie M. Predicting effects of environmental change on a migratory herbivore. *Ecosphere*. 2015;6:114.
17. Zwarts L, Wanink JH. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Neth J Sea Res*. 1993;31:441–76.
18. Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*. 2015;96:1741–53.
19. Watanabe S, Izawa M, Kato A, Ropert-Coudert Y, Naito Y. A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *App Anim Behav Sci*. 2005;94:117–31.
20. Shamoun-Baranes J, Bom R, van Loon EE, Ens BJ, Oosterbeek K, Bouten W. From sensor data to animal behaviour: an Oystercatcher example. *PLoS ONE*. 2012;7(5):e37997.
21. Fehlmann G, O'Riain MJ, Hopkins PW, O'Sullivan J, Holton MD, Shepard ELC, King AJ. Identification of behaviours from accelerometer data in a wild social primate. *Anim Biotelemetry*. 2017;5:6.
22. Watanabe YY, Takahashi A. Linking animal-borne video to accelerometers reveals prey capture variability. *Proc Natl Acad Sci*. 2013;110:2199–204.
23. Carroll G, Slip DJ, Jonsen I, Harcourt RG. Supervised accelerometry analysis can identify prey capture by penguins at sea. *J Exp Biol*. 2014. <https://doi.org/10.1242/jeb.113076>.
24. Viviant M, Trites AW, Rosen DAS, Monestiez P, Guinet C. Prey capture attempts can be detected in Steller sea lions and other marine predators using accelerometers. *Polar Biol*. 2010;33(5):713–9.
25. Ydesen KS, Wisniewska DM, Hansen JD, Beedholm K, Johnson M, Madsen PT. What a jerk: prey engulfment revealed by high-rate, supercranial accelerometry on a harbour seal (*Phoca vitulina*). *J Exp Biol*. 2014;217:2239–43.
26. Wilson AM, Lowe JC, Roskill K, Hudson PE, Golabek KA, McNutt JW. Locomotion dynamics of hunting in wild cheetahs. *Nature*. 2013;498:185–9.
27. Bom RA, Bouten W, Piersma T, Oosterbeek K, van Gils JA. Optimizing acceleration-based ethograms: the use of variable-time versus fixed-time segmentation. *Mov Ecol*. 2014;2:6.
28. Clermont J, Woodward-Gagné S, Berteaux D. Digging into the behaviour of an active hunting predator: arctic fox prey caching events revealed by accelerometry. *Mov Ecol*. 2021. <https://doi.org/10.1186/s40462-021-00295-1>.
29. Lescroëil A, Schmidt A, Elrod M, Ainley DG, Ballard G. Foraging dive frequency predicts body mass gain in the Adélie penguin. *Sci Rep*. 2021. <https://doi.org/10.1038/s41598-021-02451-4>.
30. Matthews A, Ruykys L, Ellis B, FitzGibbon S, Lunney D, Crowther MS, Glen AS, Purcell B, Moseby K, Stott J, et al. The success of GPS collar deployments on mammals in Australia. *Australian Mammalogy*. 2013;35:65–83.
31. Li X, Wang X, Fang L, Batbayar N, Natsagdorj T, Davaasuren B, Damba I, Xu Z, Cao L, Fox AD. Annual migratory patterns of Far East Greylag Geese (*Anser anser rubrirostris*) revealed by GPS tracking. *Integr Zool*. 2020;15:213–23.
32. van Gils JA, Munster VJ, Radersma R, Liefhebber D, Fouchier RAM, Klaassen M. Hampered foraging and migratory performance in swans infected with low-pathogenic Avian Influenza A virus. *PLoS ONE*. 2007;2:e184.
33. Thaxter CB, Ross-Smith VH, Clark JA, Clark NA, Conway GJ, Marsh M, Leat EH, Burton NHK. A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. *Ringed Migr*. 2014;29:65–76.
34. Hancock JA, Kushlan JA, Kahl MP. *Storks, ibises and spoonbills of the world*. London: Academic Press; 1992.
35. Lok T, Overdijk O, Tinbergen JM, Piersma T. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. *Anim Behav*. 2011;82:837–44.
36. Swennen CK, Yu YT. Food and feeding behavior of the black-faced spoonbill. *Waterbirds*. 2005;28:19–27.
37. Banos O, Galvez J-M, Damas M, Pomares H, Rojas I. Window size impact in human activity recognition. *Sensors*. 2014;14:6474–99.
38. Jouta J, Goeij PD, Lok T, Velilla E, Camphuysen CJ, Leopold M, Veer HWVD, Olff H, Overdijk O, Piersma T. Unexpected dietary preferences of Eurasian Spoonbills in the Dutch Wadden Sea: spoonbills mainly feed on small fish not shrimp. *J Ornithol*. 2018;159:839–49.
39. Enners L, Guse N, Schwemmer P, Chagas ALJ, Voigt CC, Garthe S. Foraging ecology and diet of Eurasian spoonbills (*Platalea leucorodia*) in the German Wadden Sea. *Estuar Coast Shelf Sci*. 2020;233:106539.
40. Kuipers BR. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. *Neth J Sea Res*. 1977;11:56–91.
41. Freitas V, Witte JJ, Tulp I, van der Veer HW. Shifts in nursery habitat utilization by 0-group plaice in the western Dutch Wadden Sea. *J Sea Res*. 2016;111:65–75.
42. Kuipers BR, Dapper R. Nursery function of Wadden Sea tidal flats for the brown shrimp *Crangon crangon*. *Mar Ecol-Prog Ser*. 1984;17:171–81.
43. Penning E, Govers LL, Dekker R, Piersma T. Advancing presence and changes in body size of brown shrimp *Crangon crangon* on intertidal flats in the western Dutch Wadden Sea, 1984–2018. *Mar Biol*. 2021;168(11):160.
44. Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KCJ. A flexible GPS tracking system for studying bird behaviour at multiple scales. *J Ornithol*. 2013;154:571–80.
45. Phillips RA, Xavier JC, Croxall JP. Effects of satellite transmitters on albatrosses and petrels. *Auk*. 2003;120:1082.
46. Shamoun-Baranes J, Bouten W, Van Loon EE, Meijer C, Camphuysen CJ. Flap or soar? How a flight generalist responds to its aerial environment. *Philos Trans R Soc B: Biol Sci*. 2016;371:20150395.
47. R Core Team. A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2022.
48. Ross GJ. Parametric and nonparametric sequential change detection in R: the cpm package. *J Stat Softw*. 2015;66:1–20.
49. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol*. 2006;75:1081–90.
50. Komsta L, Novomestky F. moments: Moments, cumulants, skewness, kurtosis and related tests. R package version 0.14; 2015.
51. Sur M, Suffredini T, Wessells SM, Bloom PH, Lanzone M, Blackshire S, Sridhar S, Katzner T. Improved supervised classification of accelerometry data to distinguish behaviors of soaring birds. *PLoS ONE*. 2017;12:e0174785.
52. Patterson A, Gilchrist HG, Chivers L, Hatch S, Elliott K. A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecol Evol*. 2019;9:3030–45.
53. Liaw A, Wiener M. Classification and regression by randomForest. *R News*. 2002;2:18–22.
54. Tatler J, Cassey P, Prowse TAA. High accuracy at low frequency: detailed behavioural classification from accelerometer data. *J Exp Biol*. 2018;221:jeb184085.
55. Baptist MJ, van der Wal JT, Folmer EO, Gräwe U, Elschot K. An ecotopemap of the trilateral Wadden Sea. *J Sea Res*. 2019;152:101761.
56. Pinheiro JC, Bates DM. *Mixed-effects models in S and S-Plus*. New York: Springer-Verlag; 2000.

57. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. nlme: linear and nonlinear mixed effects models. R package version 3.1–155. 2022.
58. Akaike H. Information theory and an extension of the maximum likelihood principle. In: Petran BN, Csáki F, editors. International symposium on information theory. 2nd ed. Budapest: Akadémiai Kiadó; 1973. p. 267–81.
59. Burnham K, Anderson D. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. New York: Springer-Verlag; 2002.
60. Hounslow JL, Brewster LR, Lear KO, Guttridge TL, Daly R, Whitney NM, Gleiss AC. Assessing the effects of sampling frequency on behavioural classification of accelerometer data. *J Exp Mar Biol Ecol.* 2019;512:22–30.
61. van der Veer H, Tulp I, Witte J, Poiesz S, Bolle L. Changes in functioning of the largest coastal North Sea flatfish nursery, the Wadden Sea, over the past half century. *Mar Ecol Prog Ser.* 2022;693:183–201.
62. Kuipers BR, Dapper R. Production of *Crangon crangon* in the tidal zone of the Dutch Wadden Sea. *Neth J Sea Res.* 1981;15:33–53.
63. Lok T, Veldhoen L, Overdijk O, Tinbergen JM, Piersma T. An age-dependent fitness cost of migration? Old trans-Saharan migrating spoonbills breed later than those staying in Europe, and late breeders have lower recruitment. *J Anim Ecol.* 2017;86:998–1009.
64. Adachi T, Huckstadt LA, Tift MS, Costa DP, Naito Y, Takahashi A. Inferring prey size variation from mandible acceleration in northern elephant seals. *Mar Mamm Sci.* 2019;35:893–908.
65. Brisson-Curadeau E, Elliott KH. Prey capture and selection throughout the breeding season in a deep-diving generalist seabird, the thick-billed murre. *J Avian Biol.* 2019;e01930.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

