Shorebird feeding specialists differ in how environmental conditions alter their foraging time

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Abstract

Feeding specialisation is a common cause of individual variation. Fitness payoffs of specialisation vary with environmental conditions, but the underlying behavioural mechanisms are poorly understood. Such mechanistic knowledge, however, is crucial to reliably predict responses of heterogeneous populations to environmental change. We quantified spatiotemporal allocation of foraging behaviour in wintering Eurasian oystercatchers (*Haematopus ostralegus*), a species in which feeding specialisation can be inferred from bill shape. We combined GPS and accelerometer data to quantify foraging time of 64 individuals for every tidal period in one or two winter seasons. Individuals varied widely in foraging time (3.7-6.5 hours per tidal period) and individuals that spend more time foraging had lower inferred survival. Feeding specialisation appeared a major determinant of individual variation in foraging time and its spatiotemporal allocation. Visually-hunting worm specialists foraged more during day-time and complemented intertidal foraging with grassland foraging when the exposure of intertidal flats was limited and nights were well-illuminated. Shellfish specialists increased total foraging time in cold weather, whereas foraging time of worm specialists decreased as frosty grasslands became inaccessible. Our results imply that worm specialists may be most sensitive to cold snaps and day-time disturbance, while shellfish specialists are most sensitive to high water levels. These behavioural responses can be implemented in population models to predict the vulnerability of heterogeneous populations to environmental change, and thereby provide a shortcut to long-term population studies that require fitness data across many years and conditions to make similar projections.

Introduction

Individuals vary in the expression of their mean phenotype (physiology, behaviour or demographic rate) as well as in their phenotypically plastic responses to environmental conditions. Understanding such variation is important for evolutionary and ecological dynamics. If individuals vary, and this phenotypic variation has a heritable basis and results in differential fitness, this may lead to an evolutionary response. Furthermore, individual variation can affect population dynamics, as it may cause that the mean performance of all individuals is different from the performance of an individual with the average phenotype (Bolnick et al. 2011).

One well-studied aspect in which individuals vary is feeding specialisation (Durell 2000; Bolnick et al. 2003; Araújo et al. 2011; Ceia and Ramos 2015). Commonly, individuals specialize in different foraging techniques, for example using different feeding methods to obtain the same food source, or in different diets, for example by foraging on a limited selection of food sources (Annett and Pierotti 1999; Durell 2000; Bolnick et al. 2003). Feeding specialisation may affect fitness through its effects on foraging efficiency (Terraube et al. 2014), foraging time (Cook et al. 2006) and mortality risk (Coleman and Wilson 1998; Darimont et al. 2007). Fitness consequences of specific feeding specialisations, however, may vary depending on environmental conditions and available food sources as well as competition (Goss-Custard and Durell 1988; Beukema et al. 1993; Durell 2000; Darimont et al. 2007). Such fluctuating selection pressures may promote the maintenance of feeding specialisation diversity (van de Pol et al. 2010).

Foraging time may be an important determinant of fitness associated with feeding specialisation, but how may depend on the situation. Feeding specialisations that target profitable food sources, or use an efficient feeding technique, may need little time to meet their energy requirement, and can thus shorten their foraging time (Araújo and Gonzaga 2007). However, restricted accessibility of a food source (e.g. in intertidal areas) might also limit foraging time (Durell 2000), the extent of which can vary with environmental conditions (e.g. fluctuating water levels). In such cases, foraging time is restricted to the period in which the food source is available.

Consequently, individuals with the shortest foraging time are not necessarily the most efficient individuals.

Not only total foraging time, but also the foraging time allocation may differ spatiotemporally among feeding specialisations. For example, individuals with different feeding techniques might allocate their foraging time differently over the day. Individuals that exclusively search for prey by sight are less efficient in dark nights (Sitters 2000) and, consequently, it would be expected that those individuals allocate more foraging time to the day. An individual's feeding specialisation may also influence where they forage, as various food sources occur at different places in the landscape.

Comparisons of foraging time allocation of different feeding specialisations under varying environmental conditions may reveal under which conditions individuals are most vulnerable. There are, however, very few studies that quantify foraging time differences among feeding specialisations (Grantham et al. 1995) or even among-individual variation in foraging time (Kato et al. 2000; Daunt et al. 2014). This is likely due to the need to measure a substantial number of individuals with different feeding specialisations over a prolonged period of time, representative of a wide range of environmental conditions, in all available feeding areas and during both day and night. This only recently became possible with advances in bio-logging, and specifically the combined use of accelerometers (Yoda et al. 1999) and GPS locations, enabling one to study animal behaviour continuously by simultaneously quantifying time budgets and habitat usage (e.g. Ropert-Coudert et al. 2004; Watanabe et al. 2012; Brown et al. 2013; Daunt et al. 2014).

Here, we studied the consequences of feeding specialisation for foraging time of 64 Eurasian oystercatchers (*Haematopus ostralegus*) using bio-logging for up to two non-breeding seasons in the Dutch Wadden Sea estuary. The oystercatcher is a well-studied model system for the evolution and population level consequences of feeding specialisation in the wild (Goss-Custard 1996). Oystercatchers show individual and sex-specific specialisation in foraging behaviour that result in a gradient of bill tips with different shapes (Norton-Griffiths 1967; Swennen et al. 1983; van de Pol et al. 2009). Feeding specialists range from worm and soft-shelled shellfish feeders ("worm specialists"),

with a low bill tip height, to hard-shelled shellfish feeders (“shellfish specialists”), with a high bill tip height (Durell et al. 1993; van de Pol et al. 2009). Foraging habitat is known to differ among feeding specialisations: although both worm and shellfish specialists predominantly feed on intertidal flats, worm specialists also feed on inland grasslands (Goss-Custard and Durell 1983; Caldow et al. 1999; Sitters 2000; Durell et al. 2001).

Feeding specialisation in oystercatchers may also have fluctuating fitness consequences since worm specialists had a lower survival during cold winters than shellfish specialists in the United Kingdom (Durell et al. 2001; Durell 2007), whilst a study from the Netherlands reported the opposite trend (van de Pol et al. 2010). A better understanding of the underlying mechanisms of how individuals with different feeding specialisations adapt to different environmental conditions may improve our understanding of the variety of fitness patterns previously reported or may generate new testable hypotheses on how fitness payoff may vary spatiotemporally. However, these mechanisms are at the moment poorly understood. Therefore, we investigated the following four research questions: First, how much do individuals vary in their tidal foraging time in winter? Secondly, is foraging time associated with survival? Thirdly, how much of this individual variation can be explained by feeding specialisation? Finally, do birds with different feeding specialisations allocate their foraging differently over time and space, and does this make some foraging strategies more susceptible to environmental change? We will specifically explore how foraging time depends on (a) the exposure time of intertidal areas, (b) temperature and (c) day-night patterns, as this may inform us how individuals vary in their sensitivity to respectively, global warming, sea level rise and disturbance (which mostly acts during day-time).

Materials and Methods

Study area

The study was conducted in the western Dutch Wadden Sea estuary, comprising the islands Vlieland, Texel (northern half), Griend and the surrounding intertidal flats (Figure 1). The majority of the study

area consists of intertidal flats that are accessible to oystercatchers during low tide, while inland grasslands on Texel and Vlieland provide alternative foraging sites, for example during high tide.

Data collection

We determined foraging time per tidal period (the period between two consecutive high tide moments) by equipping birds with global positioning system (GPS) trackers. Wintering oystercatchers were caught with mist nets on the western half of Vlieland in December 2016 - January 2017 (n = 20) and December 2017 (n = 42), after which they were colour-banded and equipped with GPS trackers. Birds in poor condition (<500g) and birds with noticeable bill deformities (such as crossbill, gap in bill, large asymmetry between upper and lower bill) were not equipped with a GPS tracker. None of the adult birds caught in winter were local breeding birds but bred in inland areas of the Netherlands and Germany, or in Scandinavia, which we confirmed by visually inspecting GPS tracks of the breeding season. Additionally, twenty local breeding oystercatchers were caught on the nest and equipped with trackers between May and July 2017. Eleven trackers did not generate any data (individual bird details in Supplement Table S1).

In all analyses, we used bill tip height (measured 3 mm from the bill tip using a calliper) as a continuous proxy for the type of feeding specialisation of an individual (van de Pol et al. 2009). For presenting our results in figures we used categories for visual reasons only: Worm specialists (Pointed bill shape), Intermediate (Pointed-Chisel bill shape) and Shellfish specialists (Chisel or Blunt bill shape). The corresponding bill shapes were determined in the field based on bill tip height, width and shape (van de Pol et al. 2009) and corresponded with bill tip height ranges of 2.3-3.3, 3.0-4.9 and 4.3-5.7 mm for Pointed, Pointed-Chisel and Chisel or Blunt bill shapes, respectively. The sex of a bird was determined by DNA analysis of a small blood sample taken from the wing vein. Age class (juvenile, 2nd winter or adult) was determined based on morphology (Cramp et al. 1983). Standard biometry measurements were taken, of which tarsus-toe length was used as a proxy for body size.

The UvA-BiTS GPS trackers we used collected data on both location and behaviour of birds (Bouten et al. 2013). The tracker (13.5g) included a rechargeable battery, solar panel and accelerometer and was attached on the back using a Teflon harness (2g), in total weighing 15.5g (2.00%-3.14% of the mass of the oystercatchers; mass range 494g-774g) (Figure 2a). The trackers sampled GPS positions in 5 to 60 minute interval. A 0.35 second accelerometer sample (20 Hz; tri-axial measuring surge X, sway Y and heave Z) was measured at least every ten minutes, independent of the GPS interval. GPS positions were used to determine the foraging habitat and accelerometer samples were used to classify behaviour (see below). When the battery of the tracker was empty, which happened most often between November and January, no GPS or accelerometer measurements were taken until it was recharged. All data collected by the tracker were stored on internal memory and downloaded via a radio antennae network (Bouten et al. 2013) permanently present on Vlieland during the study period. Ring readings in the study area were done throughout the year on the islands Vlieland and Texel to detect individuals with a defective tracking device. We used ring readings (registered by us and volunteers on www.wadertrack.nl) in combination with detection by the antenna system to determine apparent survival.

We annotated accelerometer data using video recordings and used a machine learning approach to classify accelerometer samples into distinct behaviours (Shamoun-Baranes et al. 2012; 2016). GPS-equipped oystercatchers were filmed on Vlieland from March-July 2017, when the tracker batteries were fully charged. The GPS tracker settings were adjusted before the filming events to record ten seconds 20Hz accelerometer samples (i.e. 200 accelerometer measurements) in 20-60s intervals (Figure 2b). Accelerometer data were synchronized with the recordings and then annotated into five behaviours (Supplement Table S2): Flying, walking, foraging, preening and inactive. Extra flight behaviour samples were selected based on GPS speed (speed >10m/s) and visual inspection of the accelerometer data (see Supplement Table S2 how flight behaviour can be easily recognized) to increase the number of flight behaviours in the annotated accelerometer dataset. Washing and aggressive behaviour were not included in the classification under the assumption that

these behaviours occurred very rarely during winter (even during the post-winter observations and filming, washing and aggressive behaviour were rarely observed).

The annotated accelerometer data were subsequently used to train a Random Forest algorithm (Breiman 2001) using summary features of the accelerometer samples (following Shamoun-Baranes et al. 2016). The annotated accelerometer data were split into 0.35 seconds samples (seven accelerometer measurements), yielding in total 33,107 annotated samples. The samples were divided into a training (24,929 samples) and a testing (8,178 samples, other individuals than training dataset) dataset to construct the classification models (Supplement Table S3). We calculated 33 statistical summary features from the accelerometer samples, which are described in Shamoun-Baranes et al. (2016; see also Supplement Table S4). The most relevant features were selected by constructing 10 decision trees using C4.5 machine learning algorithm (Quinlan, 1993), using 300 random samples of each behaviour from the training dataset. The features that occurred in the top four nodes in any of the trees were retained, while the other features were excluded. This process was done three times (Shamoun-Baranes et al. 2016). The 15 retained features (Supplement Table S4) were used to train a Random Forest with 50 trees using 1,716 samples (the minimum available for all behaviours) for all five behaviours.

The testing dataset was used to calculate the prediction accuracy of the Random Forest model. Prediction accuracy was 94.6% ($n=8,178$; $\kappa=0.927$; Supplement Table S5) and especially high for foraging, flying, inactive and preening behaviour. Walking was sometimes confused with foraging, as prey searching by sight (foraging) is identical to a slow walking behaviour and even in the field not always distinguishable. True walking behaviour, however, occurs often during the breeding season when oystercatchers tend to walk a lot inside their territory. Since our study focused on the non-breeding season we assumed that predicted walking behaviour in winter was actually most often foraging behaviour. Indeed, the pattern of foraging and walking behaviours over the tidal period was very similar (Supplement Figure S1), which would not be the case if walking often occurred during high tide (e.g. at high tide roost sites). We therefore combined foraging and walking behaviour into

one foraging class. In this study we focussed on foraging time (compared to other behaviours); our classification model distinguished foraging (including walking) from other behaviours correctly in 98.7% of all cases ($n = 8,178$; $\kappa = 0.973$; Figure 2c).

Based on GPS locations and behaviour classifications, intertidal and grassland foraging time (hours) was calculated for every bird for every tidal period (Figure 2d). A tidal period was defined as the period between two consecutive high tide moments at Vlieland Haven (Rijkswaterstaat 2018), thus each tidal period (~ 12.4 h) covered a single low tide. All behaviour measurements within a tidal period were weighed based on the interval between consecutive measurements and the intervals of foraging behaviours were summed to acquire one total foraging time estimate per tidal period.

In winter, GPS fixes were taken with hourly intervals to save battery and extra behaviour measurements were taken in between with ten minute intervals. Consequently, locations for behaviour measurements were then derived from the closest GPS fix. This did likely not strongly affect estimates of intertidal and grassland foraging time as oystercatchers did not frequently switch between the foraging habitats. Using only the GPS fixes collected with five minute intervals, we estimated that switching oystercatchers stayed on average for 21.8 consecutive hours in intertidal areas and 11.3 consecutive hours (approximately one tidal period) in grasslands.

To correct for environmental variables, daily weather data was obtained from the weather station at Vlieland (KNMI 2018). Daily moon illumination values were obtained via the *lunar.illumination* function in the *lunar* package in R.

Statistical analysis

We focused our analyses on the non-breeding season (1 August to 31 March). We omitted data if (a) it concerned the first five tidal periods after the oystercatcher was equipped with a GPS tracker ($n = 279$ tidal foraging time estimates), (b) there were less than 70 behaviour measurements in the tidal period ($n = 459$), (c) the maximum interval between two behaviour measurements was more than 20 minutes ($n = 537$), or (d) one or more GPS positions were outside the study area (Figure 1) ($n = 769$).

We subsequently removed seven birds from the analysis that had fewer than 30 tidal foraging time estimates ($n = 95$). In total, we retained 8,704 tidal foraging time estimates from 661 tidal periods and 64 birds (15, 29 and 20 worm, intermediate and shellfish specialists, respectively; Supplement Table S1).

We analysed both intertidal foraging time and total (intertidal + grassland) foraging time as a response variable. First, we examined whether foraging time was related to survival. Then, we examined which environmental factors influenced foraging time and quantified among-individual variation in foraging time. Then, we examined how much of the among-individual variation could be explained by individual traits, especially feeding specialisation, and by different foraging strategies of individuals with different feeding specialisations. All analyses were performed in R 3.3.2 (R core team, 2017).

For birds caught in winter 2016-17 and summer 2017, we investigated whether foraging time was associated with apparent survival using binary logistic regression, based on whether oystercatchers were recorded (either by GPS-tracker or ring-reading in the field) one year after release (Supplement Table S1).

We used linear mixed effects modelling to correct for environmental factors that affect intertidal and total foraging time per tidal period. Intertidal and total tidal foraging times (in hours) were separately used as response variables. Bird ID was included as random intercept. The following variables were included as explanatory variables: *Winter* (2016/17 or 2017/18), *Proportion night* (0-1, where 1 indicates that the whole tidal period was between sunset and sunrise), *Moon illumination* (0-1, where 1 is full moon) and the linear and squared terms of *Seasonday* (1 August = day 1), *Temperature* (mean daily temperature in °C), *Windspeed* (mean daily windspeed in km/h), *Proportion intertidal flat exposure* (proportion of time when water level < -10cm NAP), *Proportion intertidal flat exposure previous 10 tides* (Supplement Table S6). We included the intertidal flat exposure over the previous 10 tides to determine whether birds compensated in foraging time after prolonged periods of high water levels. The variables *Seasonday*, *Temperature* and *Windspeed* were Z-transformed prior

to analysis. We used an information theoretic model selection approach using Akaike's Information Criterion (AIC; Burnham and Anderson 2004). Models with all possible combinations of predictor variables were run and the model with the lowest AIC was selected for both the intertidal and total foraging time and used in further analyses. This approach yielded the same environmental base models as when we used backward selection based on P values, indicating that the environmental base models were not depending on the selection procedure. Full model details and P values of all variables are provided in Supplement Table S7. The residual distributions of the environmental base models (one for each of the two response variables) were visually checked for normality (Figure S2). The variance estimate of Bird ID as random intercept provided an estimate of the among-individual variation in foraging time.

Subsequently, we quantified how much the following five individual traits explained of the among-individual variation in intertidal or total foraging time by adding them to the environmental base models: (1) *Bill tip height* (mm), (2) *Sex* (Male or Female), (3) *Age class* (Juvenile (1st winter), Subadult (2nd winter) or Adult (3rd winter and older), birds can age over seasons), (4) *Tarsus-toe length* (mm, measure for bird size) and (5) *Breeding site* (local breeder on Vlieland or non-local breeder) (Supplement Table S6). Z-transformation of *Tarsus-toe length* and *Bill tip height* was applied prior to analysis. Models were constructed in which each of the traits were added singly and where all traits were added simultaneously to the environmental base models. We tested for significance of fixed terms using Wald chi-square tests by comparing models with one dropped term against the full model for the model including all individual traits. We compared the marginal R^2 (R^2_m , explained variation of fixed effects) and the conditional R^2 (R^2_c , explained variation of fixed and random effects) (Nakagawa and Schielzeth 2013) of all constructed models with the environmental base models to quantify the explained among-individual variation in foraging time by individual traits. We calculated (1) additional variation explained by fixed effects (R^2_m model - R^2_m base model), (2) individual variation not explained by individual traits (R^2_c model - R^2_m model) and (3) individual variation

explained by adding individual traits as explanatory variables ($(R^2_c \text{ base model} - R^2_m \text{ base model}) - (R^2_c \text{ model} - R^2_m \text{ model})$).

To determine whether individuals with different feeding specialisations differed in foraging time allocation, we constructed six models for intertidal and total foraging time including interactions between bill tip height and environmental factors: *Bill tip height* in interaction with (1) *Proportion low water*, (2) *Proportion low water previous 10 tides*, (3) *Temperature*, (4) *Proportion night*, (5) *Proportion night* and *Moon illumination* (three-way), and (6) all interactions mentioned before. We tested for significance of fixed terms using Wald chi-square tests by comparing models with one dropped term against the full model for the model including all interactions. We calculated additional variation explained by the fixed effects and individual variation not explained by individual traits based on R^2_m and R^2_c values (see above).

Results

Individual variation in foraging time

Mean individual foraging time ranged between 3.66 and 6.51 hours per tidal period (lower quantile = 4.18h, median = 4.62h, upper quantile = 5.14h) (Figure 3a). A total of 16.5% and 16.9% of variation in intertidal (s.d. among individuals = 0.64h) and total foraging time (s.d. = 0.62h) could be attributed to among-individual variation, respectively (Table 1). There was no indication that the amount of individual variation was inflated by sampling variance (i.e. individual variability was independent of sample size; Supplement Figure S3). All environmental variables except *Winter* were retained in the environmental base models for intertidal and total foraging time when estimating the amount of individual variation (Table 2).

Foraging time and apparent survival

Birds that were not recorded one year after they were released ($n=9$) had a longer intertidal foraging time ($\chi^2=6.2$, $df=1$, $p=0.013$) and total foraging time ($\chi^2=5.8$, $df=1$, $p=0.016$) than those that were observed ($n=20$) (Figure 3b).

Individual traits determining foraging time

Bill tip height explained 21.9% of the individual variation in total foraging time (3.7% out of 16.9% variation that could be attributed to among-individual differences; Table 1). Bill tip height significantly explained variation in total foraging time but not intertidal foraging time (Table 2, Figure 3c). Birds with a lower bill tip height foraged longer, which could be attributed to grassland foraging (Figure 3c). Intertidal foraging time was longer in young birds and local breeders but there was no variation between sexes (Table 2, Figure 3d-f). Breeding site explained 17.0% of variation of the individual variation in intertidal foraging time (2.8% out of 16.5%; Table 1). Although sex by itself explained 7.7% of individual variation in total foraging time (1.3% out of 16.9%; Table 1), it was not significant in the model with all individual traits (Table 2) as sex and bill tip height were highly correlated ($r = 0.65$). The difference between local and non-local breeders was less pronounced in total foraging time as non-local breeders foraged longer on grasslands (Table 2, Figure 3f). All five individual traits combined accounted for 26.1% (4.3% out of 16.5%) and 30.7% (5.2% out of 16.9%) of the among-individual variation for intertidal and total foraging time, respectively.

Differential responses of feeding specialisations to environmental conditions

Feeding specialists showed clear differences in foraging time responses to three environmental conditions (intertidal flat exposure, temperature and day and night) (Figure 4).

During relatively high low-tides (e.g. during bad weather) intertidal feeding areas were exposed for a shorter period than normal. Shellfish specialists' (high bill tip height) total foraging time was lower during tides with low intertidal exposure, while worm specialists (low bill tip height) slightly increased their total foraging time by grassland foraging (Figure 4b; Table 3). Worm

specialists foraged less on intertidal flats and more on grasslands when intertidal flat accessibility was limited over prolonged periods (Figure 4c, Table 3).

On cold days shellfish feeders increased their total foraging time, while foraging time of worm feeders decreased (Figure 4d; Table 3).

For all individuals, intertidal and total foraging time was longest during day-time tides (Table 2, Figure 4e). Worm specialists foraged longer than shellfish specialists during day-time tides (Figure 4e, Table 3). During the night, foraging time was similar among feeding specialisations around new moon periods, but around full moon worm feeders foraged longer which could mainly be attributed to grassland foraging (Figure 4e; Table 3).

More (6.5%) variation in total foraging time was explained by fixed variables in the model that included bill tip height in interaction with night, intertidal flat exposure and temperature than in the base model with only environmental variables (Table 1). Feeding specialisation in interaction with environmental variables explained 26.6% of among-individual variation in total foraging time (variation explained by random effect was reduced from 16.9% to 12.4%; Table 1). Environmental variables and feeding specialisation together explained 44.8% and 40.7% of variation in intertidal and total foraging time, respectively (Table 1).

Discussion

Using combined GPS and accelerometer measurements, we quantified foraging time and its spatiotemporal allocation over a wide range of environmental conditions for a substantial number (64) of individuals. We found considerable among-individual variation in foraging time. Individuals that foraged longer were less likely to be recorded again one year after they were equipped with a GPS tracker, implying a lower survival. Feeding specialisation explained a considerable part (21.9%) of the among-individual variation in total foraging time and could account for sex differences in foraging time. Most interestingly, our results show that birds with different feeding specialisations alter their foraging time differently under varying environmental conditions, suggesting they differ in their

susceptibility to environmental change. Specifically, worm specialists complemented intertidal with grassland foraging when the intertidal flats were less exposed, shortened instead of lengthened their foraging time during cold snaps and allocated more foraging time to the day.

Fitness consequences of foraging time

Individuals which forage longer under normal conditions (because of lower foraging efficiency or higher energy expenditure) are expected to be more prone to deteriorating body condition and mortality when available foraging time becomes limiting. Although foraging time of an individual can decrease through exhaustion in the period directly prior to death (Daunt et al. 2007), weak or inefficient individuals are known to forage longer to maintain or regain their body condition (Powolny et al. 2015). This is indeed supported by our finding of lower apparent survival for individuals with long foraging times. In one or two years, we should have sufficient data to more accurately estimate the effect of foraging time on true (rather than apparent) survival using capture-mark-resighting modelling on all 64 individuals.

Increased foraging time is not necessarily disadvantageous when individuals specialise in food sources that are available at different spatiotemporal scales. The intake payoffs of feeding specialisations vary depending on the environmental conditions and population structure (Svanbäck and Persson 2009; van de Pol et al. 2010). For example, specialising in a less profitable food source that is accessible for a larger proportion of time may be the best strategy when the accessibility of a more profitable food source is limited. In oystercatchers, grasslands are traditionally regarded as less profitable and, consequently, a refuge feeding habitat for weaker individuals that cannot meet their energy requirements on intertidal flats (Goss-Custard and Durell 1983; Caldow et al. 1999; Durell et al. 2001). However, worm specialists sometimes choose to feed on inland grasslands during low tide when shellfish specialists forage on intertidal flats (Figure 4a; Heppleston 1971). This suggests that grasslands cannot exclusively be regarded as a supplementary foraging habitat as under some circumstances grassland foraging appears a preferred choice of worm specialists.

376

377 *Differential susceptibility to environmental change*

378 Worm specialists complement intertidal foraging with grassland foraging when intertidal flat
379 exposure is limited by high water levels (driven by the lunar cycle or wind). By utilizing grasslands,
380 worm specialists maintain their foraging time under conditions of high water levels. Shellfish
381 specialists may lack the specialisation to feed on grasslands and hence do not feed on grasslands
382 when intertidal flat exposure is limited. To compensate for extended high water levels, and to avoid a
383 deteriorating body condition, they would need to either prolong intertidal foraging time in
384 subsequent tides or increase foraging efficiency. We found no distinct relation between shellfish
385 specialist foraging time and average intertidal exposure time over the last ten tides, suggesting that
386 shellfish specialists do not compensate in subsequent tides. This would indicate that shellfish
387 specialists may increase their foraging efficiency, for example by capturing larger prey and by
388 handling prey faster, but this comes at the cost of an increased risk of bill damage (Swennen et al.
389 1989; Rutten et al. 2006). This can explain why foraging efficiency on intertidal flats does not per se
390 differ among feeding specialisations under normal environmental conditions (Boates and Goss-
391 Custard 1989; Boates and Goss-Custard 1992; Durell et al. 1997). It is likely that worm specialists
392 maximize intertidal foraging efficiency under all conditions as capturing and eating soft-bodied prey
393 does not require specific techniques nor involves risk of bill damage (Durell et al. 1997). Shellfish
394 specialists, however, may only increase their foraging efficiency when intertidal flat accessibility is
395 limited. Winters with prolonged periods of high water levels may therefore increase mortality risk of
396 shellfish specialists. These winters are more likely to occur in the future with ongoing sea level rise
397 due to climate change (Rahmstorf 2007) and more localised effects such as soil subsidence due to
398 mining.

399 Worm specialists and shellfish specialists showed contrasting trends in foraging time with
400 temperature. As expected, shellfish specialists increased their foraging time when it was colder, likely
401 to achieve a higher food intake that is needed due to higher metabolic rates and energy expenditure

associated with colder temperatures (Kersten and Piersma 1997). An important constraint for worm specialists in cold weather conditions is that they cannot utilize grasslands, as worms and invertebrates are unreachable in frozen soil. Also, soft bodied preys on intertidal flats are more difficult to obtain under colder conditions than shellfish as they become less active (Esselink and Zwarts 1989; Zwarts and Wanink 1993). Consequently, worm specialists may be more vulnerable to cold spells as their food intake depends on intertidal foraging only. Indeed, contrary to what would be expected given the increased energy expenditure required in cold temperatures, worm specialists shorten instead of lengthen foraging time when it is cold. This suggests that foraging time is limited for worm specialists in cold weather. Our results are consistent with previous studies which found that worm specialists suffer from a higher mortality than shellfish specialists during winters with cold spells (Durell et al. 1993; 2001; Durell 2007), but it does not help us understand why a later study found the opposite trend (van de Pol et al. 2010). These results are relevant in the context of climate change, as specializing in worms is expected to become a less risky strategy in the future as cold winters may be less likely to occur.

Allocation of foraging time over day-time and night-time tides differed among feeding specialisations and also depended on the moon stage and feeding specialisation. During full moon, more foraging time was allocated to nocturnal tides (see also Heppleston 1971), probably because foraging efficiency increases in illuminated conditions compared to dark conditions (Santos et al. 2010). Interestingly, grassland foraging by worm specialists occurred mainly during night-time full moon tides, suggesting that under these conditions worm specialists can realise an intake on inland grasslands which is similar or higher than intake on intertidal flats. Many insects and worms adjust their life cycle to the moon phase (Raible et al. 2017), which has been proposed as a potential explanation for full moon grassland foraging by birds (Ydenberg et al. 1984). All birds allocated more foraging time to day-time tides, likely because waders achieve a higher foraging efficiency in daylight (Zwarts and Drent 1981; Lourenço et al. 2008). We found that worm specialists allocated approximately 1 – 1.4h (depending on moon stage) more foraging time to day-time tides compared

with shellfish specialists. This suggests that the difference in foraging efficiency between day and night is more pronounced in worm specialists, probably because they locate prey mostly visually (Ens et al. 1996). The increased reliance on day-time foraging may increase the vulnerability of worm specialists to day-time disturbance in foraging areas compared to shellfish specialists. Upon disturbance, available foraging time is shortened and energetic costs increase, which is especially costly if individuals have to compensate by foraging at times when foraging efficiency is low, as might be the case for worm specialists during the night. Consequently, we hypothesize that critical disturbance thresholds, the frequency of disturbance at which animals lose condition, are not only dependent on environmental conditions (Goss-Custard et al. 2006) but also differ between individuals with different feeding strategies.

Phenotypic plasticity in feeding specialisation is a potential mechanism via which oystercatchers anticipate changes in food availability and environmental conditions. However, individuals often consistently consume the same diet over multiple winter seasons, suggesting that their flexibility is limited (Goss-Custard and Durell 1983). The ability to switch between different feeding specialisations is likely constrained by bill morphology. For example, the longer and slender bill of females can reach more deeply buried prey like worms and thin-shelled shellfish, but is less suitable to break into the armour of thick-shelled shellfish in comparison with the shorter and higher bill of males (Hulscher and Ens 1992). Although feeding specialisations often remain consistent over winters, individuals can change their diet and bill tip shape between seasons. For example, diet switches from soft-bodied prey in summer to shellfish in early winter are documented (Boates and Goss-Custard 1989). Moreover, shellfish feeders that breed inland switch to a worm diet upon arrival in the breeding area (inducing a pointy bill shape change) and back to a shellfish diet upon arrival in the wintering area in autumn (Hulscher 1984). Although bill shape changes can take place within several weeks (Hulscher 1984), diet switches from soft-bodied prey to shellfish are likely costly since they involve a high risk of bill damage (Rutten et al. 2006). Tracking individuals over multiple years

can reveal the extent to which feeding specialisation and associated foraging time allocation strategies develop or remain similar over time.

Broader implications

By quantifying spatiotemporal foraging time using combined GPS and accelerometer measurements, we provide important insights in the behavioural mechanisms of individuals with different feeding specialisations in response to environmental conditions. In general, foraging time estimates, as quantified in this study, can be used to validate simulated foraging times in population models to determine whether virtual individuals behave similar to real individuals. Although those models ultimately focus on how body condition, survival or population numbers are affected, foraging time can also be derived for validation in individual-based models where individuals make decisions to forage during every time step (e.g. Stillman and Goss-Custard 2010). Moreover, based on behavioural adaptations we can make predictions on how vulnerable individuals are to specific environmental conditions. Being able to measure environmental susceptibility in relatively short-term studies is important as measuring actual fitness consequences often require long-term studies. For example, extremely cold winters rarely occur in Western Europe, and it has been shown that even in studies lasting multiple decades it is hard to reliably estimate how feeding specialisation in oystercatchers moderates susceptibility of adult survival to cold weather (van de Pol et al. 2010; Bailey and van de Pol 2016). Implementing behavioural responses to environmental conditions in population models may be used as a shortcut to predict responses of different feeding specialisations to environmental change.

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639

Table 1 Variation in foraging time explained by environmental base model, individual traits and by interactions of bill tip height with environmental variables. The table provides estimates of additional variation explained by fixed factors in comparison to the environmental base models (*Δ variation explained*), explained individual variation by individual traits (*Explained ind. var.*), individual variation that remains unexplained (*Unexplained ind. var.*) (see methods for calculations) and the marginal R^2 (R^2_m) and conditional R^2 (R^2_c). Explained individual variation was not calculated for models with interactions as R^2 was affected by both environmental variables and bill tip height. bth = Bill tip height.

Model	Intertidal Foraging Time					Total Foraging Time				
	Δ variation explained	Explained ind. var.	Unexplained ind. var.	R^2_m	R^2_c	Δ variation explained	Explained ind. var.	Unexplained ind. var.	R^2_m	R^2_c
environment (base model)			16.5%	0.268	0.432			16.9%	0.218	0.387
Individual traits	environment + bth	-0.2%	-0.5%	16.9%	0.266	0.435	3.8%	3.7%	13.2%	0.257
	environment + sex	-0.1%	-0.4%	16.9%	0.267	0.435	1.6%	1.3%	15.6%	0.234
	environment + age class	0.5%	0.7%	15.8%	0.273	0.430	0.1%	0.2%	16.7%	0.219
	environment + tarsus-toe	0.3%	0.0%	16.5%	0.271	0.436	0.1%	-0.1%	17.0%	0.219
	environment + breeding site	3.2%	2.8%	13.7%	0.299	0.436	1.0%	0.9%	16.0%	0.229
	environment + <i>all individual traits</i>	4.3%	4.3%	12.2%	0.311	0.432	5.4%	5.2%	11.8%	0.273
Environment responses	environment + bth*exposure	0.2%		17.1%	0.270	0.441	4.8%		13.1%	0.267
	environment + bth*10-tide exposure	0.5%		16.9%	0.273	0.442	4.8%		12.9%	0.266
	environment + bth*temp	-0.1%		16.8%	0.266	0.435	5.6%		12.3%	0.274
	environment + bth*night	1.8%		15.9%	0.286	0.445	4.1%		13.1%	0.259
	environment + bth*night*moon	1.9%		15.9%	0.287	0.446	4.4%		13.1%	0.263
	environment + <i>all bth interactions</i>	3.0%		15.0%	0.298	0.448	6.5%		12.4%	0.283

Table 2 Linear mixed model for intertidal foraging time ($R^2=0.432$) and total foraging time ($R^2=0.390$) per tidal period in hours using environmental and individual traits as explanatory variables. Environmental variables were selected based on AIC comparison of models with all possible combinations of environmental variables and using bird individual as a random intercept. Reference categories for sex, age class and breeding sites were female, adult and non-local breeder, respectively. Seasonday, temperature, windspeed, tarsus-toe and bill tip height were Z-transformed. Variance (σ^2) of the random effect, bird individual ($n=64$), was 0.307 and 0.272 for the intertidal and total foraging time models respectively.

	Intertidal Foraging Time					Total Foraging Time				
	Estimate	SE	df	χ^2	sig.	Estimate	SE	df	χ^2	sig.
<i>Intercept</i>	3.18	0.23				4.76	0.22			
Environment										
winter	-					-				
seasonday	-0.17	0.03	1	34.7	***	-0.15	0.03	1	26.9	***
seasonday ²	-0.18	0.02	1	57.3	***	-0.22	0.02	1	79.6	***
temperature	-0.23	0.04	1	32.4	***	-0.18	0.04	1	21.4	***
temperature ²	-					-				
windspeed	0.13	0.02	1	54.1	***	0.19	0.02	1	120.1	***
windspeed ²	-					0.05	0.01	1	17.9	***
exposure	7.07	0.33	1	400.9	***	6.72	0.35	1	357.7	***
exposure ²	-4.87	0.38	1	146.7	***	-5.66	0.41	1	191.0	***
10-tide exposure	6.20	0.79	1	60.0	***	2.84	0.78	1	13.1	***
10-tide exposure ²	-7.90	0.84	1	84.4	***	-5.44	0.84	1	41.7	***
night	-3.32	0.08				-3.42	0.08			
moon	-0.73	0.08				-0.96	0.08			
night*moon	1.13	0.12	1	88.5	***	2.07	0.12	1	295.7	***
Individual traits										
bill tip height	-0.02	0.09	1	0.1	ns	-0.27	0.08	1	10.5	**
sex (<i>male</i>)	-0.03	0.19	1	0.0	ns	-0.08	0.18	1	0.24	ns
age class			2	8.6	*			2	5.0	ns
<i>juvenile</i>	0.38	0.13				0.26	0.13			
<i>subadult</i>	0.14	0.09				0.06	0.09			
tarsus-toe	0.12	0.07	1	1.6	ns	0.08	0.07	1	1.6	ns
breeding site (<i>local</i>)	0.79	0.19	1	4.2	***	0.42	0.17	1	6.0	*

sig. = *: $0.05 > P > 0.01$, **: $0.01 > P > 0.001$, ***: $P < 0.001$

Table 3 Linear mixed model for intertidal foraging time and total (intertidal + grassland) foraging time per tidal period in hours using environmental factors and feeding specialization as explanatory variables, including their interaction. Environmental factors were selected based on AIC comparison of models with all possible combinations of environmental factors and using bird individual as random intercept. Seasonday, temperature, windspeed and bill tip height (bth) were Z-transformed. Variance (σ^2) of the random effect, bird individual (n=64), was 0.363 and 0.275 for intertidal and total foraging time model, respectively.

	Intertidal Foraging Time					Total Foraging Time				
	Estimate	SE	df	χ^2	sig.	Estimate	SE	df	χ^2	sig.
<i>Intercept</i>	3.26	0.21				4.89	0.21			
Environment										
winter	-					-				
seasonday	-0.14	0.03	1	25.6	***	-0.18	0.03	1	37.8	***
seasonday ²	-0.19	0.02	1	64.5	***	-0.22	0.02	1	87.6	***
temperature	-0.18	0.04				-0.16	0.04			
temperature ²	-					-				
windspeed	0.13	0.02	1	60.4	***	0.17	0.02	1	109.7	***
windspeed ²	-					0.05	0.01	1	16.2	***
exposure	7.47	0.35				6.36	0.35			
exposure ²	-5.17	0.41				-5.28	0.40			
10-tide exposure	6.68	0.78				3.31	0.78			
10-tide exposure ²	-8.39	0.84				-6.00	0.84			
night	-3.45	0.08				-3.52	0.08			
moon	-0.72	0.08				-0.98	0.08			
night*moon	1.14	0.12				2.16	0.12			
Feeding specialization										
bth	0.89	0.19				-0.90	0.19			
bth*night	0.60	0.08				0.64	0.08			
bth*moon	-0.07	0.08				0.16	0.08			
bth*night*moon	0.24	0.12	1	4.3	*	-0.71	0.12	1	37.8	***
bth*temperature	-0.07	0.02	1	8.9	**	-0.08	0.02	1	11.9	***
bth*exposure	-0.77	0.26	1	9.0	**	1.33	0.26	1	27.1	***
bth*exposure ²	0.19	0.29	1	0.4	ns	-0.71	0.72	1	10.4	**
bth*10-tide exposure	-4.23	0.72	1	34.4	***	1.46	0.77	1	1.0	ns
bth*10-tide exposure ²	4.05	0.77	1	27.7	***	-0.92	0.29	1	3.6	ns

sig. = *: $0.05 > P > 0.01$, **: $0.01 > P > 0.001$, ***: $P < 0.001$

Figure 1 Study area including the Wadden Islands Vlieland and Texel, intertidal flats and grasslands (note the small grassland area on Vlieland). On Texel only grasslands are indicated which were used by oystercatchers.

Figure 2 (a) Oystercatcher with UvA-BiTS GPS tracker showing tri-axial acceleration (X: red, Y: blue, Z: green). (b) Example of a 10s acceleration sample of a foraging bird obtained for calibration of the accelerometer. (c) Random Forest behaviour classification accuracy, separating foraging (including walking) behaviour from other behaviours. (d) Example of a time budget of one individual (intermediate specialisation) showing intertidal (IT) and grassland (GL) foraging during day and night. Tidal foraging time was calculated between two consecutive high tides (highlighted in black).

Figure 3 (a) Histogram of mean total (intertidal + grassland) foraging time per individual. Mean intertidal and grassland foraging time $\pm$ SE for total foraging time for (b) birds that were re-sighted or not re-sighted one year after the catch ($n = 29$), (c) different specialisations ($n = 64$), (d) sex ($n = 64$), (e) age class ($n = 64$) and (f) local or non-local breeding sites ($n = 64$).

Figure 4 (a) Foraging time budget examples of oystercatchers with different specialisations. Intertidal and grassland foraging time $\pm$ SE for total foraging time for different feeding specialisations for (b) different intertidal flat exposure proportions (proportion low water), (c) average intertidal flat exposure proportions over the previous 10 tides, (d) different temperatures, (e) day-time (D, proportion night = 0-0.25) and night-time (N, proportion night = 0.75-1) tidal periods in full (moon illumination = 0.75-1) and new moon (moon illumination = 0-0.25) periods. For significance of effects see Table 3.

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Supplementary Material

van der Kolk et al. (2019)
Shorebird feeding specialists differ in how environmental conditions alter their foraging time
Behavioral Ecology

Contents
Table S1-S7
Figure S1-S3

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Table S1 Overview of bird individuals tagged in this study.

Seen after 1 year: Bird was detected (by ring reading or by the antenna system) one year after catch, Y: Yes, N: No. *Local Breeder*: Breeding bird on Vlieland (Y) or elsewhere (N). *TATO*: Tarsus-toe length (mm). *Billshape*: Bill shape determined in the field based on bill tip height, bill tip width and bill tip shape, C: Chisel, H: Hammer, P: Pointed, PC: Pointed-chisel. *n_2016/17*: Number of tidal foraging time estimates in season 2016-17. *n_2017/18*: Number of tidal foraging time estimates in season 2017-18. *n_total*: Total number of tidal foraging estimates. *Included*: Included in analysis, Y: Yes, N: No.

Bird_ID	Device	Catch Date	Seen after 1 year	Sex	Birth Year	Local Breeder	TATO	BillShape	n_2016/17	n_2017/18	n_total	Included
1	5420	2-12-2016	Y	M	2015	N	94	C	147	199	346	Y
2	5423	2-12-2016	Y	M	2014	N	101	C	92	136	228	Y
3	5437	2-12-2016	Y	M	2014	N	102	C	85	47	132	Y
4	5438	2-12-2016	N	F	≤2013	N	95	PC	214	181	395	Y
5	5439	2-12-2016	N	M	2014	N	101	C	0	0	0	N
6	5435	3-12-2016	N	M	2016	N	97	C	0	0	0	N
7	5449	3-12-2016	Y	M	2016	N	96	C	222	29	251	Y
8	5450	3-12-2016	Y	F	≤2013	N	98	PC	166	0	166	Y
9	5444	5-12-2016	N	F	≤2013	N	93	PC	9	0	9	N
10	5436	18-12-2016	N	M	2016	N	95	C	66	0	66	Y
11	5445	18-12-2016	Y	F	≤2013	N	98	C	98	142	240	Y
12	5447	18-12-2016	Y	F	2015	N	99	PC	132	20	152	Y
13	5452	18-12-2016	Y	F	≤2013	N	100	P	38	0	38	Y
14	5453	18-12-2016	Y	F	2016	N	99	PC	182	0	182	Y
15	5346	18-12-2016	Y	F	≤2013	N	105	C	146	0	146	Y
16	5440	18-12-2016	Y	M	2016	N	91	C	173	191	364	Y
17	5443	18-12-2016	Y	M	2015	N	100	H	99	59	158	Y
18	5446	18-12-2016	N	F	≤2013	N	98	PC	0	0	0	N
19	5451	19-12-2016	N	F	2016	N	99	PC	98	0	98	Y
20	5424	18-1-2017	N	F	≤2013	N	95	PC	54	0	54	Y
21	5504	27-5-2017	Y	M	≤2014	Y	98	C	0	253	253	Y
22	5499	27-5-2017	Y	M	≤2014	Y	100	H	0	65	65	Y
23	5517	27-5-2017	Y	M	≤2014	Y	99	PC	0	148	148	Y
24	5512	27-5-2017	N	F	≤2014	Y	102	PC	0	0	0	N
25	5502	27-5-2017	Y	F	≤2014	Y	95	PC	0	0	0	N
26	5497	27-5-2017	N	F	≤2014	Y	101	PC	0	0	0	N
27	5509	27-5-2017	Y	F	≤2014	Y	99	PC	0	172	172	Y
28	5507	27-5-2017	Y	M	≤2014	Y	91	C	0	156	156	Y
29	5500	30-6-2017	Y	M	≤2014	Y	90	PC	0	1	1	N
30	5501	30-6-2017	N	F	≤2014	Y	96	PC	0	219	219	Y
31	5511	30-6-2017	N	F	≤2014	Y	97	P	0	45	45	Y
32	5503	1-7-2017	Y	M	≤2014	Y	97	C	0	257	257	Y
33	5505	1-7-2017	Y	F	≤2014	Y	92	PC	0	175	175	Y
34	5518	1-7-2017	Y	M	≤2014	Y	94	PC	0	243	243	Y
35	5513	1-7-2017	Y	M	≤2014	Y	96	C	0	0	0	N
36	5515	1-7-2017	N	F	≤2014	Y	102	PC	0	76	76	Y
37	5516	1-7-2017	Y	M	≤2014	Y	93	C	0	0	0	N
38	5506	1-7-2017	N	M	≤2014	Y	98	PC	0	117	117	Y
39	5514	1-7-2017	N	F	≤2014	Y	97	PC	0	227	227	Y

Table S1 (continuation) Overview of bird individuals tagged in this study.

Bird_ID	Device	Catch Date	Seen after 1 year	Sex	Birth Year	Local Breeder	TATO	BillShape	n_2016/17	n_2017/18	n_total	Included
40	5497	18-7-2017	N	F	≤2014	Y	98	PC	0	24	24	N
41	5611	15-12-2017	-	M	≤2014	N	98	PC	0	82	82	Y
42	5613	15-12-2017	-	M	2016	N	103	C	0	125	125	Y
43	5632	15-12-2017	-	M	≤2014	N	95	C	0	0	0	N
44	5633	15-12-2017	-	M	≤2014	N	99	PC	0	32	32	Y
45	5647	15-12-2017	-	F	2015	N	95	PC	0	22	22	N
46	5648	15-12-2017	-	M	≤2014	N	95	PC	0	50	50	Yes
47	5655	15-12-2017	-	F	≤2014	N	99	H	0	58	58	Y
48	5656	15-12-2017	-	F	≤2014	N	95	P	0	64	64	Y
49	5669	15-12-2017	-	F	≤2014	N	92	H	0	72	72	Y
50	5680	15-12-2017	-	M	≤2014	N	108	PC	0	98	98	Y
51	5682	15-12-2017	-	F	≤2014	N	99	PC	0	120	120	Y
52	5417	18-12-2017	-	M	≤2014	N	91	PC	0	127	127	Y
53	5486	18-12-2017	-	F	≤2014	N	103	P	0	0	0	N
54	5510	18-12-2017	-	M	2017	N	97	C	0	96	96	Y
55	5522	18-12-2017	-	F	≤2014	N	99	PC	0	2	2	N
56	5569	18-12-2017	-	M	≤2014	N	98	C	0	73	73	Y
57	5572	18-12-2017	-	M	2017	N	98	C	0	182	182	Y
58	5573	18-12-2017	-	F	2017	N	106	PC	0	153	153	Y
59	5575	18-12-2017	-	F	2016	N	97	P	0	177	177	Y
60	5577	18-12-2017	-	M	2016	N	94	PC	0	125	125	Y
61	5582	18-12-2017	-	F	≤2014	N	97	P	0	157	157	Y
62	5623	18-12-2017	-	M	≤2014	N	96	C	0	137	137	Y
63	5661	18-12-2017	-	M	2017	N	92	PC	0	0	0	N
64	5662	18-12-2017	-	F	2015	N	98	PC	0	100	100	Y
65	5424	19-12-2017	-	F	≤2014	N	95	P	0	106	106	Y
66	5452	19-12-2017	-	F	2015	N	96	PC	0	70	70	Y
67	5520	19-12-2017	-	F	2015	N	98	PC	0	133	133	Y
68	5571	19-12-2017	-	F	≤2014	N	98	P	0	120	120	Y
69	5627	19-12-2017	-	F	2016	N	96	P	0	129	129	Y
70	5631	19-12-2017	-	F	≤2014	N	97	PC	0	25	25	N
71	5637	19-12-2017	-	F	≤2014	N	95	PC	0	132	132	Y
72	5640	19-12-2017	-	F	≤2014	N	96	P	0	62	62	Y
73	5641	19-12-2017	-	F	2015	N	99	P	0	31	31	Y
74	5649	19-12-2017	-	M	≤2014	N	96	PC	0	54	54	Y
75	5652	19-12-2017	-	F	≤2014	N	97	PC	0	97	97	Y
76	5659	19-12-2017	-	F	≤2014	N	96	P	0	134	134	Y
77	5660	19-12-2017	-	F	≤2014	N	98	P	0	66	66	Y
78	5677	19-12-2017	-	F	≤2014	N	93	P	0	65	65	Y
79	5678	19-12-2017	-	F	≤2014	N	98	P	0	101	101	Y
80	5679	19-12-2017	-	F	≤2014	N	98	PC	0	80	80	Y
81	5683	19-12-2017	-	F	≤2014	N	100	PC	0	12	12	N
82	5685	19-12-2017	-	F	≤2014	N	93	P	0	127	127	Y

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714 **Table S2** Overview, description and example of behaviours used for annotating raw accelerometer data.

Behaviour	Forage	Walk	Fly	Inactive	Preen
Description	Searching, handling and eating prey	Walking and running without signs of foraging (e.g. in territory)	Flight	Sleeping or (motionless) alert behaviour	Preening feathers
ACC signal example
Time (1 second, 20 ACC samples in each graph)					

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718 **Table S3** Number of samples in Training and Testing datasets for classification model for 0.35s accelerometer
719 samples. See details of Bird ID in Table S1.

			Forage	Walk	Fly	Inactive	Preen
<i>Train</i>	Bird ID	7	5671	495	1776	6660	2368
		27	2237	494	144	2633	371
		29	743	727	211	397	2
	Total		8651	1716	2131	9690	2741
<i>Random Forest Input</i>			1716	1716	1716	1716	1716
<i>Test</i>	Bird ID	4			927		
		11	30	166		955	608
		14				1031	278
		38	1063	118	81	507	
		39	1603	167	72	326	246
	Total		2696	451	1080	2819	1132

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722 **Table S4** Feature selection for Random Forest model for behaviour classification. For description of feature
723 selection see main text. For description of features see Table S1 in Shamoun-Baranes et al., 2016.

Feature	Selected
mean_x	selected
mean_y	selected
mean_z	selected
std_x	selected
std_y	selected
std_z	selected
mean_pitch	selected
std_pitch	selected
mean_roll	not selected
std_roll	selected
correlation_xy	not selected
correlation_yz	not selected
correlation_xz	selected
meanabsder_x	selected
meanabsder_y	selected
meanabsder_z	not selected
noise_x	not selected
noise_y	not selected
noise_z	not selected
noise/absder_x	not selected
noise/absder_y	not selected
noise/absder_z	not selected
fundfreq_x	not selected
fundfreq_y	not selected
fundfreq_z	not selected
odba	selected
vedba	not selected
fundfreqcorr_x	not selected
fundfreqcorr_y	not selected
fundfreqcorr_z	not selected
fundfreqmagnitude_x	selected
fundfreqmagnitude_y	not selected
fundfreqmagnitude_z	selected

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725 **Table S5** Test results for random forest classification model using five different behaviours.

		Predicted					<i>Recall</i>
		Forage	Walk	Fly	Inactive	Preen	
Actual	Forage	2474	205	5	1	11	0.92
	Walk	42	397	11	0	1	0.88
	Fly	1	53	1026	0	0	0.95
	Inactive	7	2	0	2720	90	0.96
	Preen	6	8	0	2	1116	0.99
	<i>Precision</i>	0.98	0.60	0.98	1.00	0.92	

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729 **Table S6** Environmental variables and individual traits included as explanatory variables in the analysis.

Variable	Type	Description
winter	Environment	Winter of tracking: 2016/17 or 2017/18
seasonday	Environment	Day in the season, Day 1 = August 1
temperature	Environment	Daily mean temperature in °C
windspeed	Environment	Daily mean windspeed in km/h
exposure	Environment	Proportion of time with water level < -10cm NAP
10-tide exposure	Environment	Proportion of time with water level < -10cm NAP in the previous 10 tides
night	Environment	Proportion night (0 - 1), 1 indicates that whole tidal period was between sunset and sunrise
moon	Environment	Moon illumination (0 – 1), 1 is a full moon
bill tip height	Individual	Bill tip height in mm, measured 3mm from the bill tip
sex	Individual	Sex: male or female
age class	Individual	Juvenile (1st winter), subadult (2nd winter), adult (3rd winter and older)
tarsus-toe	Individual	Tarsus-toe length in mm
breeding site	Individual	Breeding on Vlieland (local breeder) or elsewhere (non-local breeder)

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Table S7 Full model with environmental variables for intertidal and total foraging time. Highlighted in red are variables that were excluded in model selection. The same variables were excluded when using model selection based on AIC and backward selection based on P values. P values were obtained using Wald chi-square tests comparing models with one dropped term against the full model.

	Intertidal Foraging Time					Total Foraging Time				
	Estimate	SE	df	χ^2	P	Estimate	SE	df	χ^2	P
<i>Intercept</i>	3.35	0.22				4.73	0.22			
winter	0.02	0.06	1	0.1	0.73	0.11	0.06	1	3.1	0.08
seasonday	-0.15	0.04	1	14.5	0.0001	-0.14	0.04	1	12.0	<0.0001
seasonday ²	-0.20	0.03	1	45.1	<0.0001	-0.23	0.03	1	60.3	<0.0001
temperature	-0.21	0.04	1	22.3	<0.0001	-0.18	0.04	1	16.9	<0.0001
temperature ²	0.01	0.03	1	0.2	0.63	0.00	0.03	1	0.0	0.9
windspeed	0.12	0.02	1	49.5	<0.0001	0.18	0.02	1	114.8	<0.0001
windspeed ²	0.01	0.01	1	0.6	0.44	0.05	0.01	1	16.4	<0.0001
exposure	7.16	0.36	1	394.9	<0.0001	6.68	0.35	1	350.4	<0.0001
exposure	-4.99	0.42	1	139.6	<0.0001	-5.61	0.42	1	179.0	<0.0001
10-tide exposure	6.25	0.79	1	62.1	<0.0001	3.04	0.79	1	14.9	<0.0001
10-tide exposure ²	-7.99	0.85	1	87.3	<0.0001	-5.68	0.85	1	44.9	<0.0001
night	-3.32	0.08				-3.42	0.08			
moon	-0.73	0.08				-0.96	0.08			
night*moon	1.14	0.12	1	89.1	<0.0001	2.07	0.12	1	296.7	<0.0001

Figure S1 Mean foraging time s.s. (a) and walking time s.s. (b) over the tidal stage for birds with different feeding specialisations. For the analysis, foraging time was calculated as foraging time s.s. + walking time s.s..

Figure S2 Residual distributions of the environmental base models for intertidal foraging time (a-b) and total foraging time (c-d).

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Figure S3 Mean foraging time (hour) against sample size (number of tidal foraging time estimates) for all 64 individuals included in this study.

750 **References**

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