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

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

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21 Movement ecology

22 **Abstract**

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

42 **Introduction**

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

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

61 Foraging time may be an important determinant of fitness associated with feeding
62 specialisation, but how may depend on the situation. Feeding specialisations that target profitable
63 food sources, or use an efficient feeding technique, may need little time to meet their energy
64 requirement, and can thus shorten their foraging time (Araújo and Gonzaga 2007). However,
65 restricted accessibility of a food source (e.g. in intertidal areas) might also limit foraging time (Durell
66 2000), the extent of which can vary with environmental conditions (e.g. fluctuating water levels). In
67 such cases, foraging time is restricted to the period in which the food source is available.

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

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

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

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

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

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

115

116 **Materials and Methods**

117 *Study area*

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

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

122

123 *Data collection*

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

135 In all analyses, we used bill tip height (measured 3 mm from the bill tip using a calliper) as a
136 continuous proxy for the type of feeding specialisation of an individual (van de Pol et al. 2009). For
137 presenting our results in figures we used categories for visual reasons only: Worm specialists
138 (Pointed bill shape), Intermediate (Pointed-Chisel bill shape) and Shellfish specialists (Chisel or Blunt
139 bill shape). The corresponding bill shapes were determined in the field based on bill tip height, width
140 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
141 4.3-5.7 mm for Pointed, Pointed-Chisel and Chisel or Blunt bill shapes, respectively. The sex of a bird
142 was determined by DNA analysis of a small blood sample taken from the wing vein. Age class
143 (juvenile, 2nd winter or adult) was determined based on morphology (Cramp et al. 1983). Standard
144 biometry measurements were taken, of which tarsus-toe length was used as a proxy for body size.

145 The UvA-BiTS GPS trackers we used collected data on both location and behaviour of birds
146 (Bouten et al. 2013). The tracker (13.5g) included a rechargeable battery, solar panel and
147 accelerometer and was attached on the back using a Teflon harness (2g), in total weighing 15.5g
148 (2.00%-3.14% of the mass of the oystercatchers; mass range 494g-774g) (Figure 2a). The trackers
149 sampled GPS positions in 5 to 60 minute interval. A 0.35 second accelerometer sample (20 Hz; tri-
150 axial measuring surge X, sway Y and heave Z) was measured at least every ten minutes, independent
151 of the GPS interval. GPS positions were used to determine the foraging habitat and accelerometer
152 samples were used to classify behaviour (see below). When the battery of the tracker was empty,
153 which happened most often between November and January, no GPS or accelerometer
154 measurements were taken until it was recharged. All data collected by the tracker were stored on
155 internal memory and downloaded via a radio antennae network (Bouten et al. 2013) permanently
156 present on Vlieland during the study period. Ring readings in the study area were done throughout
157 the year on the islands Vlieland and Texel to detect individuals with a defective tracking device. We
158 used ring readings (registered by us and volunteers on www.wadertrack.nl) in combination with
159 detection by the antenna system to determine apparent survival.

160 We annotated accelerometer data using video recordings and used a machine learning
161 approach to classify accelerometer samples into distinct behaviours (Shamoun-Baranes et al. 2012;
162 2016). GPS-equipped oystercatchers were filmed on Vlieland from March-July 2017, when the
163 tracker batteries were fully charged. The GPS tracker settings were adjusted before the filming
164 events to record ten seconds 20Hz accelerometer samples (i.e. 200 accelerometer measurements) in
165 20-60s intervals (Figure 2b). Accelerometer data were synchronized with the recordings and then
166 annotated into five behaviours (Supplement Table S2): Flying, walking, foraging, preening and
167 inactive. Extra flight behaviour samples were selected based on GPS speed (speed >10m/s) and visual
168 inspection of the accelerometer data (see Supplement Table S2 how flight behaviour can be easily
169 recognized) to increase the number of flight behaviours in the annotated accelerometer dataset.
170 Washing and aggressive behaviour were not included in the classification under the assumption that

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

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

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

197 one foraging class. In this study we focussed on foraging time (compared to other behaviours); our
198 classification model distinguished foraging (including walking) from other behaviours correctly in
199 98.7% of all cases (n= 8,178; $\kappa=0.973$; Figure 2c).

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

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

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

216

217 *Statistical analysis*

218 We focused our analyses on the non-breeding season (1 August to 31 March). We omitted data if (a)
219 it concerned the first five tidal periods after the oystercatcher was equipped with a GPS tracker (n =
220 279 tidal foraging time estimates), (b) there were less than 70 behaviour measurements in the tidal
221 period (n = 459), (c) the maximum interval between two behaviour measurements was more than 20
222 minutes (n = 537), or (d) one or more GPS positions were outside the study area (Figure 1) (n = 769).

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

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

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

238 We used linear mixed effects modelling to correct for environmental factors that affect
239 intertidal and total foraging time per tidal period. Intertidal and total tidal foraging times (in hours)
240 were separately used as response variables. Bird ID was included as random intercept. The following
241 variables were included as explanatory variables: *Winter* (2016/17 or 2017/18), *Proportion night* (0-1,
242 where 1 indicates that the whole tidal period was between sunset and sunrise), *Moon illumination*
243 (0-1, where 1 is full moon) and the linear and squared terms of *Seasonday* (1 August = day 1),
244 *Temperature* (mean daily temperature in °C), *Windspeed* (mean daily windspeed in km/h), *Proportion*
245 *intertidal flat exposure* (proportion of time when water level < -10cm NAP), *Proportion intertidal flat*
246 *exposure previous 10 tides* (Supplement Table S6). We included the intertidal flat exposure over the
247 previous 10 tides to determine whether birds compensated in foraging time after prolonged periods
248 of high water levels. The variables *Seasonday*, *Temperature* and *Windspeed* were Z-transformed prior

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

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

274 explained by adding individual traits as explanatory variables (R^2_c base model - R^2_m base model) –
275 (R^2_c model - R^2_m model)).

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

285

286 **Results**

287 *Individual variation in foraging time*

288 Mean individual foraging time ranged between 3.66 and 6.51 hours per tidal period (lower quantile =
289 4.18h, median = 4.62h, upper quantile = 5.14h) (Figure 3a). A total of 16.5% and 16.9% of variation in
290 intertidal (s.d. among individuals = 0.64h) and total foraging time (s.d. = 0.62h) could be attributed to
291 among-individual variation, respectively (Table 1). There was no indication that the amount of
292 individual variation was inflated by sampling variance (i.e. individual variability was independent of
293 sample size; Supplement Figure S3). All environmental variables except *Winter* were retained in the
294 environmental base models for intertidal and total foraging time when estimating the amount of
295 individual variation (Table 2).

296

297 *Foraging time and apparent survival*

298 Birds that were not recorded one year after they were released (n=9) had a longer intertidal foraging
299 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
300 observed (n=20) (Figure 3b).

301

302 *Individual traits determining foraging time*

303 Bill tip height explained 21.9% of the individual variation in total foraging time (3.7% out of 16.9%
304 variation that could be attributed to among-individual differences; Table 1). Bill tip height
305 significantly explained variation in total foraging time but not intertidal foraging time (Table 2, Figure
306 3c). Birds with a lower bill tip height foraged longer, which could be attributed to grassland foraging
307 (Figure 3c). Intertidal foraging time was longer in young birds and local breeders but there was no
308 variation between sexes (Table 2, Figure 3d-f). Breeding site explained 17.0% of variation of the
309 individual variation in intertidal foraging time (2.8% out of 16.5%; Table 1). Although sex by itself
310 explained 7.7% of individual variation in total foraging time (1.3% out of 16.9%; Table 1), it was not
311 significant in the model with all individual traits (Table 2) as sex and bill tip height were highly
312 correlated ($r = 0.65$). The difference between local and non-local breeders was less pronounced in
313 total foraging time as non-local breeders foraged longer on grasslands (Table 2, Figure 3f). All five
314 individual traits combined accounted for 26.1% (4.3% out of 16.5%) and 30.7% (5.2% out of 16.9%) of
315 the among-individual variation for intertidal and total foraging time, respectively.

316

317 *Differential responses of feeding specialisations to environmental conditions*

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

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

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

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

328 For all individuals, intertidal and total foraging time was longest during day-time tides (Table
329 2, Figure 4e). Worm specialists foraged longer than shellfish specialists during day-time tides (Figure
330 4e, Table 3). During the night, foraging time was similar among feeding specialisations around new
331 moon periods, but around full moon worm feeders foraged longer which could mainly be attributed
332 to grassland foraging (Figure 4e; Table 3).

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

340

341 **Discussion**

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

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

353

354 *Fitness consequences of foraging time*

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

364 Increased foraging time is not necessarily disadvantageous when individuals specialise in
365 food sources that are available at different spatiotemporal scales. The intake payoffs of feeding
366 specialisations vary depending on the environmental conditions and population structure (Svanbäck
367 and Persson 2009; van de Pol et al. 2010). For example, specialising in a less profitable food source
368 that is accessible for a larger proportion of time may be the best strategy when the accessibility of a
369 more profitable food source is limited. In oystercatchers, grasslands are traditionally regarded as less
370 profitable and, consequently, a refuge feeding habitat for weaker individuals that cannot meet their
371 energy requirements on intertidal flats (Goss-Custard and Durell 1983; Caldow et al. 1999; Durell et
372 al. 2001). However, worm specialists sometimes choose to feed on inland grasslands during low tide
373 when shellfish specialists forage on intertidal flats (Figure 4a; Heppleston 1971). This suggests that
374 grasslands cannot exclusively be regarded as a supplementary foraging habitat as under some
375 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

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

416 Allocation of foraging time over day-time and night-time tides differed among feeding
417 specialisations and also depended on the moon stage and feeding specialisation. During full moon,
418 more foraging time was allocated to nocturnal tides (see also Heppleston 1971), probably because
419 foraging efficiency increases in illuminated conditions compared to dark conditions (Santos et al.
420 2010). Interestingly, grassland foraging by worm specialists occurred mainly during night-time full
421 moon tides, suggesting that under these conditions worm specialists can realise an intake on inland
422 grasslands which is similar or higher than intake on intertidal flats. Many insects and worms adjust
423 their life cycle to the moon phase (Raible et al. 2017), which has been proposed as a potential
424 explanation for full moon grassland foraging by birds (Ydenberg et al. 1984). All birds allocated more
425 foraging time to day-time tides, likely because waders achieve a higher foraging efficiency in daylight
426 (Zwarts and Drent 1981; Lourenço et al. 2008). We found that worm specialists allocated
427 approximately 1 – 1.4h (depending on moon stage) more foraging time to day-time tides compared

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

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

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

455

456 *Broader implications*

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

474

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494

495 **References**

- 496 Annett CA, Pierotti R. 1999. Long-term reproductive output in western gulls: consequences of alternate tactics
497 in diet choice. *Ecology*. 80:288-297.
- 498 Araújo MS, Gonzaga MO. 2007. Individual specialisation in the hunting wasp *Trypoxylon (Trypargilum)*
499 *albonigrum* (Hymenoptera, Crabronidae). *Behav Ecol Sociobiol*. 61:1855-1863.
- 500 Araújo MS, Bolnick DI, Layman CA. 2011. The ecological causes of individual specialisation. *Ecol Lett*. 14:948-
501 958.
- 502 Bailey LD, van de Pol M. 2016. Tackling extremes: challenges for ecological and evolutionary research on
503 extreme climatic events. *J Anim Ecol*. 85:85-96.

504 Beukema JJ, Essink K, Michaelis H, Zwarts L. 1993. Year-to-year variability in the biomass of macrobenthic
505 animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Neth J Sea Res.*
506 31:319-330.

507 Boates JS, Goss-Custard JD. 1989. Foraging behaviour of oystercatchers *Haematopus ostralegus* during a diet
508 switch from worms *Nereis diversicolor* to clams *Scrobicularia plana*. *Can J Zool.* 67:2225-2231.

509 Boates JS, Goss-Custard JD. 1992. Foraging behaviour of oystercatchers *Haematopus ostralegus* specializing on
510 different species of prey. *Can J Zool.* 70:2398-2404.

511 Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML. 2003. The ecology of individuals:
512 incidence and implications of individual specialisation. *Am Nat.* 161:1-28.

513 Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC,
514 Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol.* 26:183-
515 192.

516 Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KC. 2013. A flexible GPS tracking system for studying
517 bird behaviour at multiple scales. *J Ornithol.* 154:571-580.

518 Breiman L. 2001. Random forests. *Mach Learn.* 45:5-32.

519 Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP. 2013. Observing the unwatchable through acceleration
520 logging of animal behavior. *Anim Biotelemetry.* 1:20.

521 Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol*
522 *Method Res.* 33:261-304.

523 Caldow RWG, Goss-Custard JD, Stillman RA, Durell SLVD, Swinfen R, Bregnballe T. 1999. Individual variation in
524 the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and
525 susceptibility to interference. *J Anim Ecol.* 68:869-878.

526 Ceia FR, Ramos JA. 2015. Individual specialisation in the foraging and feeding strategies of seabirds: a review.
527 *Mar Biol.* 162:1923-1938.

528 Coleman K, Wilson DS. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-
529 specific. *Anim Behav.* 56:927-936.

530 Cook TR, Cherel Y, Tremblay Y. 2006. Foraging tactics of chick-rearing Crozet shags: individuals display
531 repetitive activity and diving patterns over time. *Polar Biol.* 29:562-569.

532 Cramp S, Simmons KLE, Brooks DC, Collar NJ, Dunn E, Gillmor R, Hollom PAD, Hudson R, Nicholson EM, Ogilvie
533 MA, Olney PJS, Roselaar CS, Voous KH, Wallace DIM, Wattel J, Wilson MG. 1983. Handbook of the birds of
534 Europe, the Middle East and North Africa. The birds of the Western Palearctic: 3. Waders to gulls. Oxford,
535 United Kingdom: Oxford University Press.

536 Darimont CT, Paquet PC, Reimchen TE. 2007. Stable isotopic niche predicts fitness of prey in a wolf–deer
537 system. *Biol J Linn Soc.* 90:125-137.

538 Daunt F, Afanasyev V, Adam A, Croxall JP, Wanless S. 2007. From cradle to early grave: juvenile mortality in
539 European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biol*
540 *Letters.* 3:371-374.

541 Daunt F, Reed TE, Newell M, Burthe S, Phillips RA, Lewis S, Wanless S. 2014. Longitudinal bio-logging reveals
542 interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. *Ecology.* 95:2077-
543 2083.

544 Durell SLVD, Goss-Custard JD, Caldow RWG. 1993. Sex-related differences in diet and feeding method in the
545 oystercatcher *Haematopus ostralegus*. *J Anim Ecol.* 62:205-215.

546 Durell SLVD, Goss-Custard JD, Perez-Hurtado A. 1997. The efficiency of juvenile oystercatchers *Haematopus*
547 *ostralegus* feeding on ragworm *Nereis diversicolor*. *Oceanographic Literature Review.* 9:1019.

548 Durell SLVD. 2000. Individual feeding specialisation in shorebirds: population consequences and conservation
549 implications. *Biol Rev.* 75:503-518.

550 Durell SLVD, Goss-Custard JD, Caldow RW, Malcolm HM, Osborn D. 2001. Sex, diet and feeding method-related
551 differences in body condition in the Oystercatcher *Haematopus ostralegus*. *Ibis.* 143:107-119.

552 Durell SLVD. 2007. Differential survival in adult Eurasian oystercatchers *Haematopus ostralegus*. *J Avian Biol.*
553 38:530-535.

554 Ens BJ, Bunscoeke EJ, Hoekstra R, Hulscher JB, Kersten M, DeVlas SJ. 1996. Prey choice and search speed: why
555 simple optimality fails to explain the prey choice of oystercatchers *Haematopus ostralegus* feeding on
556 *Nereis diversicolor* and *Macoma balthica*. *Ardea.* 84:73-90.

557 Esselink P, Zwarts L. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis*
558 *diversicolor*. *Mar Ecol Prog Ser.* 56:243-254.

559 Goss-Custard JD, Durell SLVD. 1983. Individual and age differences in the feeding ecology of Oystercatchers
560 *Haematopus ostralegus* wintering on the Exe Estuary, Devon. *Ibis.* 125:155-171.

561 Goss-Custard JD, Durell SLVD. 1988. The effect of dominance and feeding method on the intake rates of
562 oystercatchers, *Haematopus ostralegus*, feeding on mussels. *J Anim Ecol.* 57:827-844.

563 Goss-Custard JD. 1996. *The Oystercatcher: from individuals to populations (Vol. 7)*. Oxford, United Kingdom:
564 Oxford University Press.

565 Goss-Custard JD, Triplet P, Sueur F, West AD. 2006. Critical thresholds of disturbance by people and raptors in
566 foraging wading birds. *Biol Conserv.* 127:88-97.

567 Grantham ÖK, Moorhead DL, Willig MR. 1995. Foraging strategy of the giant rams-horn snail, *Marisa*
568 *cornuarietis*: an interpretive model. *Oikos.* 72:333-342.

569 Hephleston PB. 1971. The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in northern
570 Scotland. *J Anim Ecol.* 40:651-672.

571 Hulscher JB. 1984. Growth and abrasion of the oystercatcher bill in relation to dietary switches. *Neth J Zool.*
572 35:124-154.

573 Hulscher JB, Ens BJ. 1992. Is the bill of the male Oystercatcher a better tool for attacking mussels than the bill
574 of the female. *Neth J Zool.* 42:85-100.

575 Kato A, Watanuki Y, Nishiumi I, Kuroki M, Shaughnessy P, Naito Y. 2000. Variation in foraging and parental
576 behavior of king cormorants. *Auk.* 117:718-730.

577 Kersten M, Piersma T. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an
578 energetically expensive way of life. *Ardea.* 75:175-187.

579 KNMI. 2018. Daggegevens van het weer in Nederland. [https://www.knmi.nl/nederland-
580 nu/klimatologie/daggegevens/](https://www.knmi.nl/nederland-nu/klimatologie/daggegevens/). Visited 2018-09-01.

581 Lourenço PM, Silva A, Santos CD, Miranda AC, Granadeiro JP, Palmeirim JM. 2008. The energetic importance of
582 night foraging for waders wintering in a temperate estuary. *Acta Oecol.* 34:122-129.

583 Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R² from generalized linear mixed-
584 effects models. *Methods Ecol Evol.* 4:133-142.

585 Norton-Griffiths M. 1967. Some ecological aspects of the feeding behaviour of the oystercatcher *Haematopus*
586 *ostralegus* on the edible mussel *Mytilus edulis*. *Ibis.* 109:412-424.

587 Powolny T, Eraud C, Masson JD, Bretagnolle V. 2015. Vegetation structure and inter-individual distance affect
588 intake rate and foraging efficiency in a granivorous forager, the Eurasian Skylark *Alauda arvensis*. *J Ornithol.*
589 156:569-578.

590 Quinlan JR. 1993. C4.5 Programs for Machine Learning. San Mateo, California: Morgan Kaufmann Publishers.

591 R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for
592 Statistical Computing.

593 Rahmstorf S. 2007. A semi-empirical approach to projecting future sea-level rise. *Science*. 315:368-370.

594 Raible F, Takekata H, Tessmar-Raible K. 2017. An overview of monthly rhythms and clocks. *Front Neurol*. 8:189.

595 Ropert-Coudert Y, Grémillet D, Kato A, Ryan PG, Naito Y, Le Maho Y. 2004. A fine-scale time budget of Cape
596 gannets provides insights into the foraging strategies of coastal seabirds. *Anim Behav*. 67:985-992.

597 Rutten AL, Oosterbeek K, Ens BJ, Verhulst S. 2006. Optimal foraging on perilous prey: risk of bill damage
598 reduces optimal prey size in oystercatchers. *Behav Ecol*. 17:297-302.

599 Rijkswaterstaat. 2018. Waterinfo. <https://waterinfo.rws.nl/>. Visited 2018-09-01.

600 Santos CD, Miranda AC, Granadeiro JP, Lourenço PM, Saraiva S, Palmeirim JM. 2010. Effects of artificial
601 illumination on the nocturnal foraging of waders. *Acta Oecol*. 36:166-172.

602 Shamoun-Baranes J, Bom R, van Loon EE, Ens BJ, Oosterbeek K, Bouten W. 2012. From sensor data to animal
603 behaviour: an oystercatcher example. *PloS one*. 7:e37997.

604 Shamoun-Baranes J, Bouten W, van Loon EE, Meijer C, Camphuysen CJ. 2016. Flap or soar? How a flight
605 generalist responds to its aerial environment. *Phil Trans R Soc B*. 371:20150395.

606 Sitters HP. 2000. The role of night-feeding in shorebirds in an estuarine environment with specific reference to
607 mussel-feeding oystercatchers. Doctoral dissertation, University of Oxford.

608 Stillman RA, Goss-Custard JD. 2010. Individual-based ecology of coastal birds. *Biological Reviews*. 85:413-434.

609 Svanbäck R, Persson L. 2009. Population density fluctuations change the selection gradient in Eurasian perch.
610 *Am Nat*. 173:507-516.

611 Swennen CLLM, De Bruijn LLM, Duiven P, Leopold MF, Marteiijn ECL. 1983. Differences in bill form of the
612 Oystercatcher *Haematopus ostralegus*; a dynamic adaptation to specific foraging techniques. *Neth J Sea*
613 *Res*. 17:57-83.

614 Swennen CLLM, Leopold MF, De Bruijn LLM. 1989. Time-stressed oystercatchers, *Haematopus ostralegus*, can
615 increase their intake rate. *Anim Behav*. 38:8-22.

616 Terraube J, Guixé D, Arroyo B. 2014. Diet composition and foraging success in generalist predators: Are
617 specialist individuals better foragers? *Basic Appl Ecol*. 15:616-624.

618 van de Pol M, Ens BJ, Oosterbeek K, Brouwer L, Verhulst S, Tinbergen JM, Rutten AL, Jong MD. 2009.
619 Oystercatchers' bill shapes as a proxy for diet specialisation: more differentiation than meets the eye.
620 *Ardea*. 97:335-347.

621 van de Pol M, Brouwer L, Ens BJ, Oosterbeek K, Tinbergen JM. 2010. Fluctuating selection and the maintenance
622 of individual and sex-specific diet specialisation in free-living oystercatchers. *Evolution*. 64:836-851.

623 van der Kolk H, Ens BJ, Oosterbeek K, Bouten W, Allen AM, Frauendorf M, Lameris TK, Oosterbeek T, Deuzeman
624 S, de Vries K, Jongejans E, van de Pol M. 2019. Data from: shorebird feeding specialists differ in how
625 environmental conditions alter their foraging time. Dryad Digital Repository.
626 <https://doi.org/10.5061/dryad.73n5tb2sb>

627 Watanabe S, Sato K, Ponganis PJ. 2012. Activity time budget during foraging trips of emperor penguins. *PloS*
628 *one*. 7:e50357.

629 Ydenberg RC, Prins HT, Van Dijk J. 1984. A lunar rhythm in the nocturnal foraging activities of wintering
630 barnacle geese. *Wildfowl*. 35:93-96.

631 Yoda K, Sato K, Niizuma Y, Kurita M, Bost C, Le Maho Y, Naito Y. 1999. Precise monitoring of porpoising
632 behaviour of Adélie penguins determined using acceleration data loggers. *J Exp Biol*. 202:3121-3126.

633 Zwarts L, Drent RH. 1981. Prey depletion and the regulation of predator density: Oystercatchers (*Haematopus*
634 *ostralegus*) feeding on Mussels (*Mytilus edulis*). In: Jones NV, Wolff WJ. *Feeding and Survival Strategies of*
635 *Estuarine Organisms*. Boston, Massachusetts: Springer. p. 193-216.

636 Zwarts L, Wanink JH. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the
637 variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates.
638 *Neth J Sea Res*. 31:441-476.

639

640 **Table 1** Variation in foraging time explained by environmental base model, individual traits and by interactions
641 of bill tip height with environmental variables. The table provides estimates of additional variation explained by
642 fixed factors in comparison to the environmental base models (*Δ variation explained*), explained individual
643 variation by individual traits (*Explained ind. var.*), individual variation that remains unexplained (*Unexplained*
644 *ind. var.*) (see methods for calculations) and the marginal R^2 (R^2_m) and conditional R^2 (R^2_c). Explained individual
645 variation was not calculated for models with interactions as R^2 was affected by both environmental variables
646 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	0.389
	environment + sex	-0.1%	-0.4%	16.9%	0.267	0.435	1.6%	1.3%	15.6%	0.234	0.387
	environment + age class	0.5%	0.7%	15.8%	0.273	0.430	0.1%	0.2%	16.7%	0.219	0.387
	environment + tarsus-toe	0.3%	0.0%	16.5%	0.271	0.436	0.1%	-0.1%	17.0%	0.219	0.389
	environment + breeding site	3.2%	2.8%	13.7%	0.299	0.436	1.0%	0.9%	16.0%	0.229	0.389
	environment + <i>all individual traits</i>	4.3%	4.3%	12.2%	0.311	0.432	5.4%	5.2%	11.8%	0.273	0.390
Environment responses	environment + bth*exposure	0.2%		17.1%	0.270	0.441	4.8%		13.1%	0.267	0.397
	environment + bth*10-tide exposure	0.5%		16.9%	0.273	0.442	4.8%		12.9%	0.266	0.395
	environment + bth*temp	-0.1%		16.8%	0.266	0.435	5.6%		12.3%	0.274	0.397
	environment + bth*night	1.8%		15.9%	0.286	0.445	4.1%		13.1%	0.259	0.390
	environment + bth*night*moon	1.9%		15.9%	0.287	0.446	4.4%		13.1%	0.263	0.394
	environment + <i>all bth interactions</i>	3.0%		15.0%	0.298	0.448	6.5%		12.4%	0.283	0.407

647

648 **Table 2** Linear mixed model for intertidal foraging time ($R^2=0.432$) and total foraging time ($R^2=0.390$) per tidal
649 period in hours using environmental and individual traits as explanatory variables. Environmental variables
650 were selected based on AIC comparison of models with all possible combinations of environmental variables
651 and using bird individual as a random intercept. Reference categories for sex, age class and breeding sites were
652 female, adult and non-local breeder, respectively. Seasonday, temperature, windspeed, tarsus-toe and bill tip
653 height were Z-transformed. Variance (σ^2) of the random effect, bird individual ($n=64$), was 0.307 and 0.272 for
654 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			
<i>Environment</i>										
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	***
<i>Individual traits</i>										
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. = *: $0.05 > P > 0.01$, **: $0.01 > P > 0.001$, ***: $P < 0.001$

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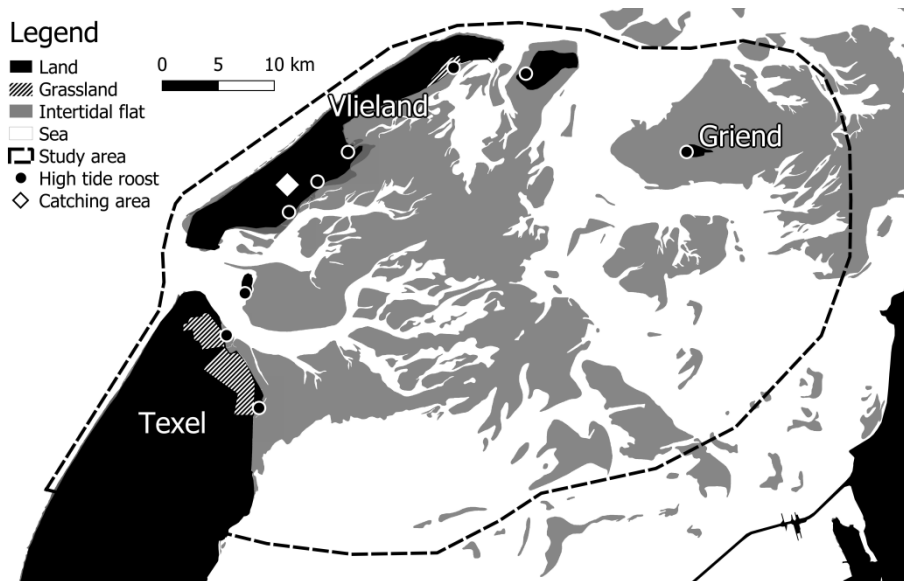
657 **Table 3** Linear mixed model for intertidal foraging time and total (intertidal + grassland) foraging time per tidal
658 period in hours using environmental factors and feeding specialization as explanatory variables, including their
659 interaction. Environmental factors were selected based on AIC comparison of models with all possible
660 combinations of environmental factors and using bird individual as random intercept. Seasonday, temperature,
661 windspeed and bill tip height (bth) were Z-transformed. Variance (σ^2) of the random effect, bird individual
662 (n=64), was 0.363 and 0.275 for intertidal and total foraging time model, respectively.
663

	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			
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			
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

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

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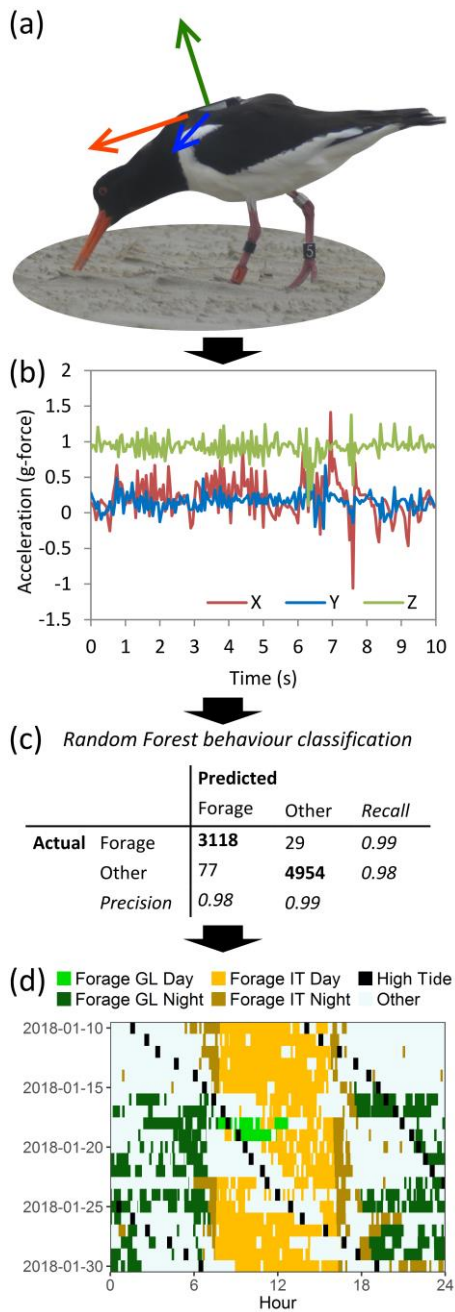


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668 **Figure 1** Study area including the Wadden Islands Vlieland and Texel, intertidal flats and grasslands

669 (note the small grassland area on Vlieland). On Texel only grasslands are indicated which were used

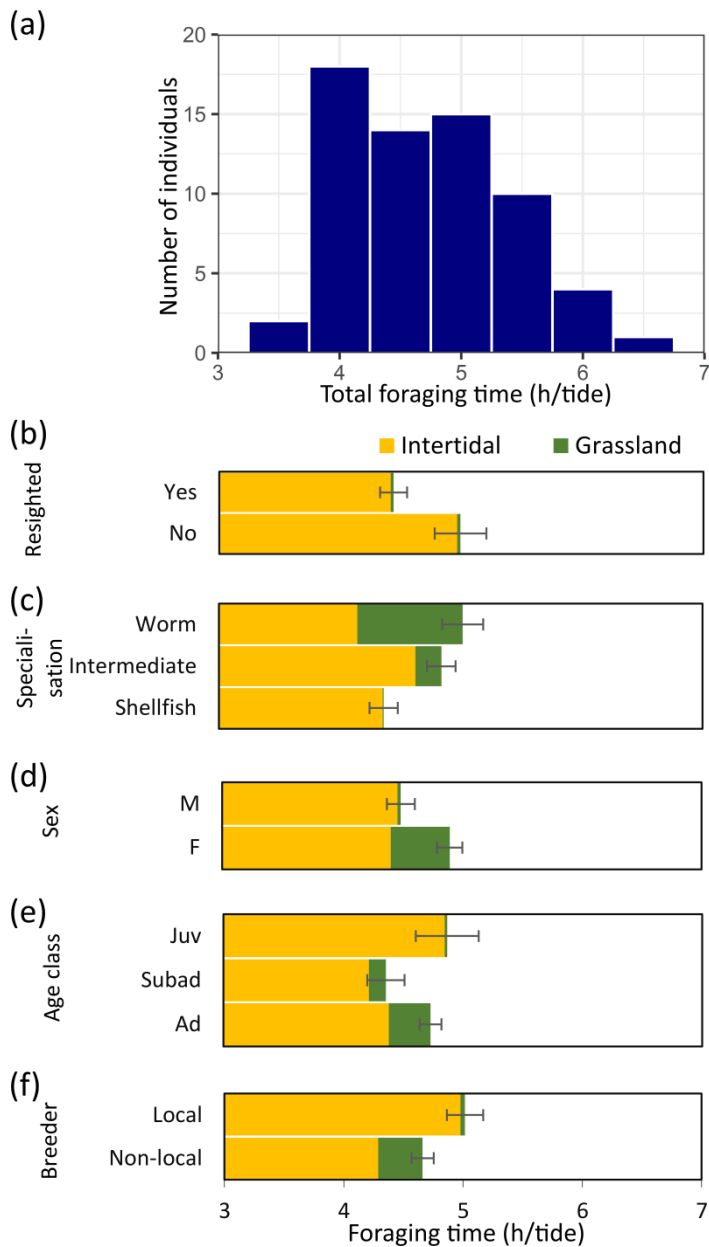
670 by oystercatchers.



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

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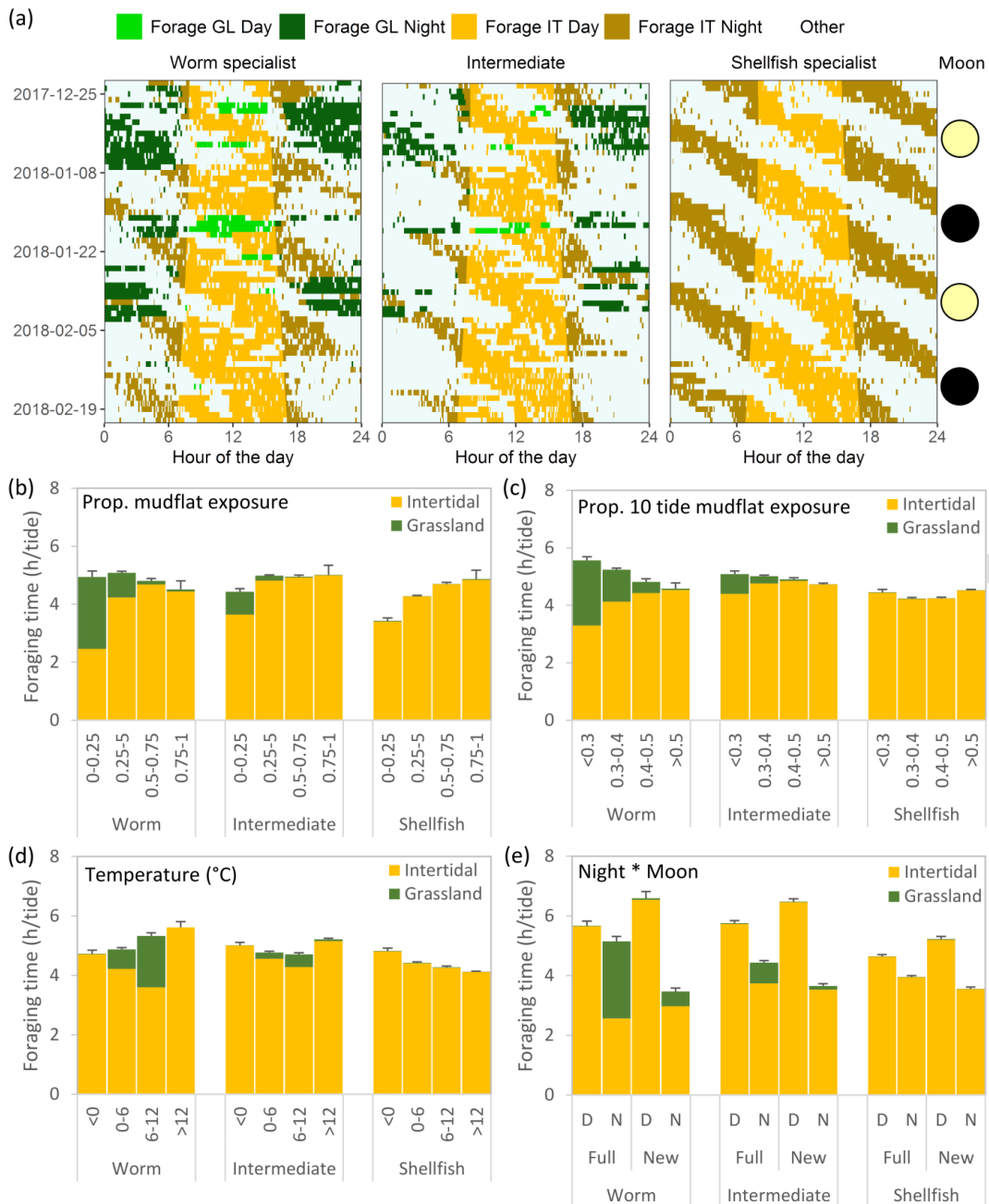


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680 **Figure 3** (a) Histogram of mean total (intertidal + grassland) foraging time per individual. Mean
 681 intertidal and grassland foraging time \pm SE for total foraging time for (b) birds that were re-sighted or
 682 not re-sighted one year after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

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687 **Figure 4** (a) Foraging time budget examples of oystercatchers with different specialisations. Intertidal
 688 and grassland foraging time \pm SE for total foraging time for different feeding specialisations for (b)
 689 different intertidal flat exposure proportions (proportion low water), (c) average intertidal flat
 690 exposure proportions over the previous 10 tides, (d) different temperatures, (e) day-time (D,
 691 proportion night = 0-0.25) and night-time (N, proportion night = 0.75-1) tidal periods in full (moon
 692 illumination = 0.75-1) and new moon (moon illumination = 0-0.25) periods. For significance of effects
 693 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

POST PRINT

705 **Table S1** Overview of bird individuals tagged in this study.
706 *Seen after 1 year*: Bird was detected (by ring reading or by the antenna system) one year after catch, Y: Yes, N:
707 No. *Local Breeder*: Breeding bird on Vlieland (Y) or elsewhere (N). *TATO*: Tarsus-toe length (mm). *Billshape*: Bill
708 shape determined in the field based on bill tip height, bill tip width and bill tip shape, C: Chisel, H: Hammer, P:
709 Pointed, PC: Pointed-chisel. *n_2016/17*: Number of tidal foraging time estimates in season 2016-17.
710 *n_2017/18*: Number of tidal foraging time estimates in season 2017-18. *n_total*: Total number of tidal foraging
711 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	<i>Forage</i>	<i>Walk</i>	<i>Fly</i>	<i>Inactive</i>	<i>Preen</i>
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					
<i>X (Surge):</i> Red					
<i>Y (Sway):</i> Blue					
<i>Z (Heave):</i> Green					
	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>			<i>1716</i>	<i>1716</i>	<i>1716</i>	<i>1716</i>	<i>1716</i>
<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					
		Forage	Walk	Fly	Inactive	Preen	Recall
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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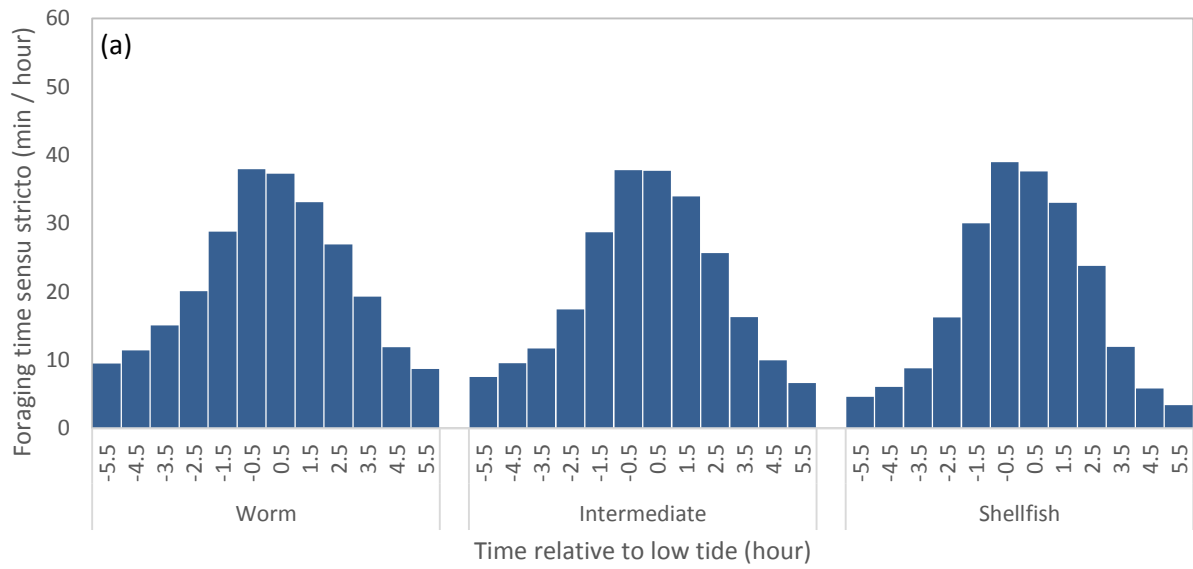
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732 **Table S7** Full model with environmental variables for intertidal and total foraging time. Highlighted in red are
 733 variables that were excluded in model selection. The same variables were excluded when using model selection
 734 based on AIC and backward selection based on P values. P values were obtained using Wald chi-square tests
 735 comparing models with one dropped term against the full model.

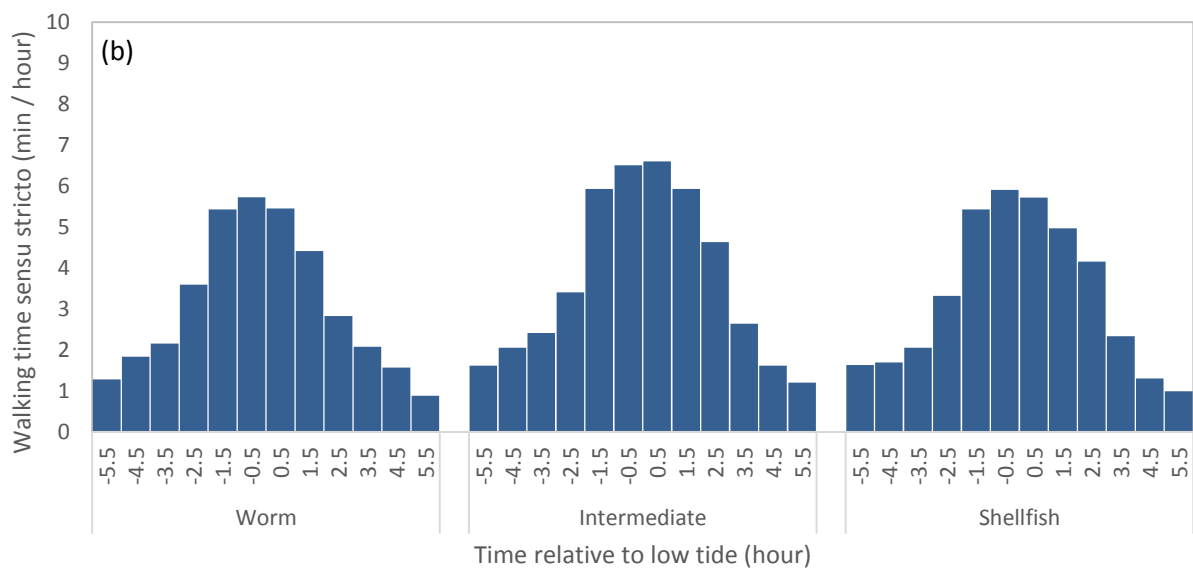
	Intertidal Foraging Time					Total Foraging Time				
	Estimate	SE	df	χ^2	P	Estimate	SE	df	χ^2	P
<i>Intercept</i>	3.35	0.22				4.73	0.22			
winter	0.02	0.06	1	0.1	0.73	0.11	0.06	1	3.1	0.08
seasonday	-0.15	0.04	1	14.5	0.0001	-0.14	0.04	1	12.0	<0.0001
seasonday ²	-0.20	0.03	1	45.1	<0.0001	-0.23	0.03	1	60.3	<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

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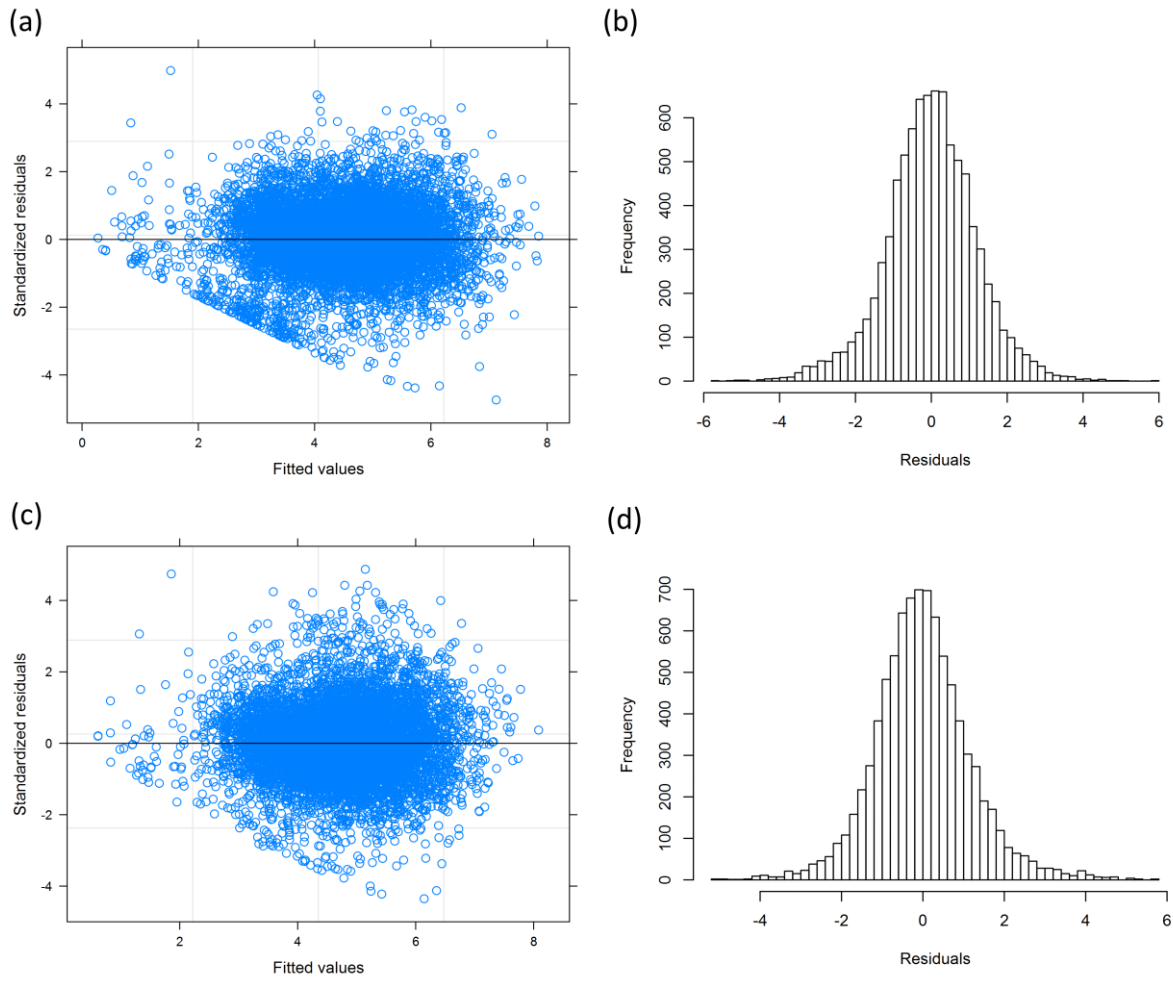
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740 **Figure S1** Mean foraging time s.s. (a) and walking time s.s. (b) over the tidal stage for birds with different
 741 feeding specialisations. For the analysis, foraging time was calculated as foraging time s.s. + walking time s.s..

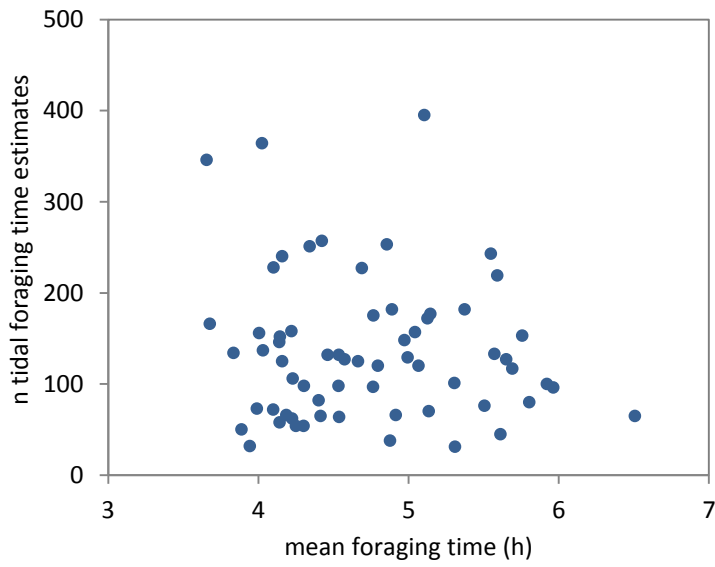
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744 **Figure S2** Residual distributions of the environmental base models for intertidal foraging time (a-b) and total
 745 foraging time (c-d).

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

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750 **References**

751 Shamoun-Baranes J, Bouten W, van Loon EE, Meijer C, Camphuysen CJ. 2016. Flap or soar? How a flight
752 generalist responds to its aerial environment. *Phil Trans R Soc B*. 371:20150395.

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