



Relative effects of static and dynamic abiotic conditions on foraging behaviour in breeding Sandwich terns

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ABSTRACT: Where and when animals forage depends on the spatio-temporal distribution and catchability of their prey. In dynamic environments, animals can repeatedly target areas that provide predictable availability of prey or may search for ephemeral conditions of high prey availability. However, how foraging behaviour is initiated in response to static versus dynamic environmental conditions is difficult to study, since both environmental data sources are often lacking. In this study, central-place foraging Sandwich terns were tracked using GPS loggers during foraging. Hidden Markov models showed that the probability of switching between transit and foraging was most strongly affected by the static variable sediment type. Wave period (a dynamic variable related to weather), salinity (a dynamic variable) and water depth (another static variable) affected the transition probability to a lesser extent. Cloud cover, wind speed and current speed were only included in lower ranked models. Air and water temperature were not included in any model. Consistent with the greater importance of static versus dynamic abiotic conditions, consistency between foraging trips of the same individual varied irrespective of tidal, diurnal or seasonal cycles, although trips made close in time within a season were slightly more similar than trips with a larger time gap. We suggest that Sandwich terns target broad areas with coarser sediments, where sandeels (*Ammodytidae*) are more common, and that weather variables may be related to prey visibility. Our study suggests that even in highly dynamic environments, static environmental variables may more strongly affect foraging behaviour of coastal seabirds than dynamic variables.

KEY WORDS: *Thalasseus sandvicensis* · Seabird · Sandeel · Hidden Markov model · GPS · Dynamic time warping · Central place foraging

1. INTRODUCTION

How animals move to obtain food for survival and reproduction is a central topic in ecology (Hays et al. 2016, Joo et al. preprint doi:10.48550/arXiv.2006.00110). Foraging animals are generally expected to

match their distribution to the distribution of their prey to maximize energy gain (Stephens & Krebs 1986). Many animals also act as 'central place foragers', making repeated trips to and from a central area (Orians & Pearson 1979). For example, breeding seabirds need to return to their terrestrial nesting site

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after each foraging trip (Buckley & Buckley 1980). The central place foraging strategy represents an additional energetic burden while travelling between breeding and foraging areas to adequately provision offspring as well as themselves (Burke & Montevecchi 2009). During each foraging trip, seabirds must relocate their prey in a highly dynamic, 3-dimensional, fluid environment. Species have therefore evolved specific foraging strategies and patch-choice rules that are often driven by the occurrence of favourable biotic and/or abiotic conditions that lead them to available food resources (Weimerskirch et al. 1993, Hamer et al. 2001, Watanuki et al. 2008, Ventura et al. 2020). The aforementioned studies, however, almost exclusively focus on describing foraging cues of larger seabirds in oceanic environments. How smaller seabirds in coastal ecosystems initiate foraging in relation to the environment is less well known.

In such dynamic environments, where the distribution of prey availability may change quickly, foragers need to adapt their foraging movements accordingly (Weimerskirch et al. 2005). Coastal waters are inherently dynamic due to varying water depths and sediment types, the tidal cycle, currents, fronts and high local turbidity at the discharges of rivers (Smout et al. 2013, Thaxter et al. 2013, Goyert 2015, Robertson et al. 2016, Marinao et al. 2019). When both prey and predator species rely on dynamic habitats, predators are expected to show a strong behavioural response to ephemeral environmental conditions that may indicate prey availability and to vary their at-sea area use according to the spatial and temporal scales at which environmental conditions change. For example, seabird foraging congregations (Embling et al. 2012, Cox et al. 2013), chick-provisioning rates at the colonies (Stienen et al. 2000) and individual seabirds' foraging site selection (Trevail et al. 2019) have been linked to tidal cycles. In addition, seabird foraging is also driven by windscape (De Pascalis et al. 2020, Ventura et al. 2020), turbidity (Baptist & Leopold 2010, Kowalczyk et al. 2015) and currents/eddies (Hyrenbach et al. 2006, Scales et al. 2014). Studying the response of individual seabird movements to dynamic environmental covariates is challenging, as it requires *concurrent* data on both topics (Ogburn et al. 2017).

Many seabird species forage only in relatively close proximity to the coast. One of these is the piscivorous Sandwich tern *Thalasseus sandvicensis* (Latham, 1787), a species with a mean maximum foraging range of 25–30 km during the breeding season (Fijn et al. 2017). In the North Sea, Sandwich terns specialize in feeding on a few pelagic fish species

(sandeel Ammodytidae spp., Atlantic herring *Clupea harengus* and European sprat *Sprattus sprattus*; Veen 1977, Stienen et al. 2000), particularly during chick rearing (Courstens et al. 2017). In general, Sandwich terns only bring one prey item back to the chick per foraging trip, a strategy called 'single-prey loading' (Stienen et al. 2015, Gaglio et al. 2018). Despite this diet specialization, substantial variation in foraging site selection within and between individual Sandwich terns (Fijn et al. 2017, Perrow et al. 2017) suggests that prey become available unpredictably in space and time or occur at predictable combinations of environmental factors but at varying locations at different times. If and how Sandwich terns respond to static and dynamic environmental conditions, and how they adjust their foraging movements in response to tidal, diurnal and seasonal cycles, has not been studied in detail before.

In this study, we used the Sandwich tern as a model species to study how breeding seabirds foraging in dynamic coastal ecosystems initiate and stop foraging in response to static and dynamic environmental variables. We studied the foraging trips of Sandwich terns breeding along the Dutch North Sea coast during late incubation and chick-rearing using GPS-logger data and information on environmental variables. The foraging area of these birds covers the south-western part of the Dutch coastal zone (Fijn et al. 2017), which is a large river delta that has a variety of water depths and sediment types, where river discharge causes frontal zones, and the tidal cycle has a large influence on currents. First, we aimed to quantify the relative importance of static (sediment type, water depth) and dynamic variables that fluctuate spatially and over the season (salinity, water temperature), within the tidal cycle (water level, water current speed) and due to weather (wind speed, air temperature, cloud cover) on the probability of Sandwich terns switching from transit flights to foraging and back. Second, we aimed to quantify individual spatial consistency (i.e. the similarity between foraging trips) across 3 temporal scales (tidal cycles, time of day since sunrise and day of year). Considering the strong effect of the tidal cycle on chick provisioning rates, the lengths of sandeels brought to the chicks (Stienen et al. 2000) and the importance of sediment grain size for sandeels (Holland et al. 2005, van der Kooij et al. 2008, Tien et al. 2017), we hypothesized that predictors of prey availability, such as sediment type, water depth, tidal currents and turbidity, will mainly predict the start of foraging behaviour in Sandwich terns. We expected more dynamic factors such as weather conditions to have

less of an effect on foraging behaviour, since these will have more of an influence on the foraging efficiency of terns rather than patch choice. Furthermore, we expected individuals to revisit the same areas during specific phases of the tidal cycle, thereby reducing the spatial consistency relative to time of day and day of the year.

2. MATERIALS AND METHODS

2.1. Deployment of tracking devices

In May and June 2012–2015 and 2017, 48 adult Sandwich terns were captured in the Natura 2000-Special Protection Area Haringvliet located in the south-western part of the Netherlands. In 2012, 2013, 2015 and 2017, the breeding colony was located at the Scheelhoek (51° 49' N, 4° 4' E), whereas in 2014, the colony was located at the Slijkplaat (51° 48' N, 4° 9' E), 5 km to the east. Both colonies were in freshwater, respectively 2.5 and 7.5 km away from the sea and together held between 1500 and 3300 pairs annually between 2012 and 2017. Breeding birds were captured on the nest with walk-in traps during the last week of incubation (based on laying date of this synchronously breeding species) or with spring traps during chick-rearing (chicks up to 2 wk old). Birds were ringed with a uniquely numbered metal ring and a field-readable darvic colour-ring.

All birds were equipped with a GPS logger (Eco-tone GPS-UHF loggers, ~4 g, length × width × height: 35 × 15 × 10 mm) that recorded date, time, GPS position and speed at 5 min intervals but differed in power supply. Most loggers had a single-use battery that allowed up to ~400 GPS fixes on one battery load, depending on environmental conditions and sampling intervals. Eight loggers (3 in 2013, 2 in 2014, 3 in 2017) were equipped with solar panels, allowing data recording until the loggers fell off due to the degradation of the harness material. Data were automatically transferred via UHF to base stations placed in the colony from a distance up to ~100 m. In 2012–2013, loggers were programmed to collect data for 6 h d⁻¹ to save battery power and increase the longevity of the logger, while in later seasons devices were programmed with cycles of 12–16 h to allow data collection over the entire day.

In 2012, 7 of these loggers were attached to feathers on the back of the terns with TESA tape (No. 4651; Beiersdorf) following Wilson et al. (1997). Sandwich terns were aggressive towards the tape deployments, and some removed their logger by

plucking and biting the taped feathers, resulting in premature loss of 4 out of 7 tags. In 2017, we deployed 4 tags with superglue (Loctite Superglue) following successful deployments in the UK with this methodology (Collier et al. 2017), but again tag loss occurred within 1 wk. The remaining 37 loggers were attached with a backpack loop harness following Kenward (1985). The harness was constructed from fishing elastic (Preston Innovations Slip Elastic, diameter: 1.4–2.2 mm), which made the harness strong and flexible but also ensured that the harness was shed after 2–3 mo due to degradation by sunlight and saltwater (R. C. Fijn et al. unpubl. data). Using the harness instead of tape or glue reduced handling time (capture to release) from approximately 15 min to 10 min. In a follow-up project on Sandwich terns with the same tagging methods, R. M. W. Green et al. (unpubl. data) showed long-term tag effects where loggers were deployed with a harness compared to glue-mounted loggers (lower return rates in subsequent years), yet foraging behaviour of birds with glue and harness deployments proved not to differ. The weight of the loggers, rings and harness material (5.8 g) was within the generally accepted limit of 3% of the body mass (Phillips et al. 2003, Vandenabeele et al. 2011) of the Sandwich terns in our study (average weight: 241 ± 13.4 g; range: 210–270 g; ~2.4%).

2.2. GPS data, trip definition and home range

A total of 34 out of 48 loggers successfully transferred positional data to the base station placed in the colony. Nine loggers were lost before they transferred any data, and the fate of the remaining 5 loggers is unknown. These loggers may have encountered technical failures or birds may have deserted the colony after deployment. The resulting data was classified into 'trips' based on 2 criteria: (1) the bird was ≥2.5 km from the colony centre (which is where outbound terns enter the North Sea by crossing the Haringvlietsluizen) or (2) there was a time gap of >30 min between locations. Trips were considered completely recorded when they started and ended at the colony.

All analyses were carried out in R version 4.1.2 (R Core Team 2021). Utilization density (UD) kernels were estimated to define a combined home range for all tracked individuals. UD kernels were estimated using a smoothing factor of 2 km and a grid cell size of 1 km, using the R package 'adehabitatHR' version 0.4.19 (Calenge 2006).

2.3. Hidden Markov models for behavioural classification

Behavioural states and the probabilities of switching between states were determined using a hidden Markov model (HMM), which classifies track segments based on speed and relative turning angle (Langrock et al. 2012, McClintock & Michelot 2018). As this process requires a constant sampling rate, tracking data was selected from loggers that were pre-set to sample at 5 min intervals and in which the resulting intervals were not longer than 6 min. As timestamps in the original tracking data were rounded to minutes, selected data included intervals up to 6.5 min. In total, 6 min intervals accounted for 13% of the data. HMMs generally assume regular time intervals between subsequent positions, as variability introduces noise in derived track characteristics—particularly in step lengths. Variability in time intervals resulted in, on average, 114 m longer step length in 6 min interval data ($\beta_{6\text{-min}} = 0.07$, $t = 3.2$, $p = 0.001$) and fitting a 3-state HMM using data with only 5 min intervals led to very similar distributions of step length and turning angles and the same classifications of behavioural states in 100% ($n_{\text{positions}} = 13918$) of all positions and 100% ($n_{\text{positions}} = 11554$) of positions with 5 min intervals. However, we did not resample data to regular intervals because we were mainly interested in environmental covariates at specific locations and times. The R package 'MOMENTUHMM' version 1.5.4 (McClintock & Michelot 2018) was used to fit a 3-state HMM using a gamma distribution for step lengths and a von Mises distribution for turning angles. In HMMs, the number of states as well as starting values must be defined *a priori*. We used the following starting values: for the mean step size, $\mu_{\text{step}} = 5250$ and 1500 m; for the concentration parameter of the turning angles, $\varphi_{\text{angle}} = 0.7$, 0.9 and 2. We varied these initial parameters to test the sensitivity of the model results to starting value selection. A 3-state model was specified because foraging trips of seabirds typically consist of (1) outbound and inbound flights between foraging areas and the colony (commuting), (2) searching and foraging (foraging) and (3) resting at the colony or elsewhere (resting). We predicted commuting to be characterized by high travel speeds and strongly directional flight paths; foraging to be characterized by slower travel speeds and sinuous turning angles; and resting to be characterized by travel speeds of (nearly) zero and random turning angles. After fitting the model, the Viterbi algorithm was used to assign the most likely state to each step (Morales et al. 2004, McClintock & Michelot 2018).

2.4. Environmental covariates

For each position, the following covariates were retrieved. Median grain size of the sediment (μm) was extracted from the Deltares website (<https://opendap.deltares.nl/thredds/catalog/opendap/tno/ncp/catalog.html>) for the Dutch Continental Shelf, and from the VLIZ website (<https://www.vliz.be>; Verfaillie et al. 2006) for the Belgian Continental Shelf. The following modelled abiotic data was generated by the 3D water movement and water quality (TRIWAQ) model (<https://www.svasek.nl/en/model-research/waqua/>; see Supplement 1 at www.int-res.com/articles/suppl/m692p137_supp.pdf for more background information on this model): water depth (m), water current speed at the surface (N m^{-2}), salinity at the surface (PSU), water temperature at the surface ($^{\circ}\text{C}$), wave height (m), wave period (s), wind speed (m s^{-1}), air temperature ($^{\circ}\text{C}$) and cloud cover (%). The TRIWAQ model simulates hydrostatic water movement in 3 dimensions (Adema 2019) and has a temporal (output) resolution of 1 h and a spatial resolution of 300–500 m (thus, much smaller than most foraging or transit step sizes; see Section 3.1). Abiotic conditions at the GPS position/time combinations of tagged birds as well as at random points were extracted from the TRIWAQ model results. All covariates were standardized using the 'standardize' package version 0.2.2 in R so that all had a mean of 0 and a standard deviation of 1 (Eager 2017). To aid in interpretation of the results, we plotted the values for 6 sample locations (see Figs. S4 & S5 in Supplement 2) and categorized the spatial variability and the temporal variability at 3 temporal scales (seasonal, day-to-day, diurnal). Variance inflation factors (VIFs) indicated strong multicollinearity for wave height (VIF = 5.8), which was therefore removed. Among the remaining covariates, VIFs ranged from 1.0 for sediment median grain size to 2.5 for water depth; thus, below what is generally considered 'severe' multicollinearity (VIF > 3; Zuur et al. 2010).

2.5. Model setup and comparison

Using tracking data for which all covariates were available, a 3-state model without covariate effects on the transition probabilities was fitted. Exploration of this first model showed that almost all positions classified by this model as resting were in the colony or on land. As we were interested in foraging at sea and not near the colony (where short, undirected movements may also occur), we constrained the model to prevent switching from the resting to the

foraging state; a commuting flight was thus always required before foraging. To include this constraint, we refitted the 3-state model while fixing the transition probabilities between resting and foraging to (virtually) zero (the ‘null’ model). Next, we added covariate effects on the switching and stationary probabilities (Iorio-Merlo et al. 2022). Since we were only interested in what environmental covariates affected foraging behaviour, only covariate effects on transition probabilities between transit and foraging were estimated; others were fixed to zero. The effect of covariates (without interactions) on transition probabilities was modelled via a multinomial logit link function, following Michelot et al. (2016). To deal with autocorrelation in step lengths, the length of the previous step was included as a covariate on the current step length (Lawler et al. 2019). We subsequently fitted all potential models ($n = 512$, including an intercept-only model) and performed model selection based on Akaike’s information criterion (AIC). We present results for models with $\Delta\text{AIC} < 2$.

Individuals can differ in their response to the environment, and therefore repeated observations of the same individual represent a source of non-independence in the data. In the R package ‘MOMENTUHMM’, individual-level effects on the transition probabilities can be included by estimating 2 or more ‘mixtures’ — sets of transition probabilities — and a probability for each individual to be in a particular mixture (McClin-tock & Michelot 2018). Here, we allowed for 2 and 3 mixtures in the final model and evaluated whether adding mixtures improved model fits using AIC.

2.6. Individual consistency

To study the consistency with which individuals revisit the same areas on different foraging trips and how this consistency changes across different temporal scales (seasonal, diurnal and tidal), we performed pairwise comparisons of GPS tracks of complete foraging trips from the same individual. Similarity in geometry and distance between trips was quantified using dynamic time warping (DTW), which identifies the path between 2 tracks with the smallest distance to the 2 comparison tracks, using the ‘SimilarityMeasures’ package version 1.4 (Toohey 2015). Lower DTW values correspond to greater similarity between trips. DTW correlates strongly with other measures of similarity, such as the commonly used nearest-neighbour analysis, but is often more sensitive to differences between trajectories and has the advantage of being symmetrical: the DTW between trip A

and B is the same as between trip B and A (Cleasby et al. 2019). We calculated the DTW between all trips of the same individual, and log-transformed DTW to deal with non-normality. To answer the question of whether spatial consistency was higher for trips that occur in the same phase of the tidal cycle, at the same time of day or on closer dates, we calculated the time differences between the trips in their (1) time to high tide (in min), (2) time since sunrise (in min) and (3) date (in days). Subsequently, we used log DTW as the response variable in a range of generalized linear mixed-effects models (GLMMs), fitted with integrated nested Laplace approximation (INLA) using the R-INLA package version 21.11.22 (Lindgren & Rue 2015) with a random intercept for each individual, and with the 3 covariates of time differences included as random walk order 2 effects. Importance of the explanatory variables time to high tide, time to sunrise and day of year was assessed by comparing the Watanabe-Akaike Information Criterion (WAIC).

2.7. Sample size of final data set

Out of the 34 loggers that transferred data to the base station, 4 had very small sample sizes in terms of number of positions ($n = 2, 2, 5$ and 33) or number of trips ($n = 1$). These data were excluded from the analysis. Another individual had data at 15 min intervals and was therefore excluded. This led to data from a total of 28 individuals. The final data set used for the HMM and the data set for the consistency analyses differed, as only data with environmental covariates were used for the HMM and only complete trips were included in the consistency analysis (Table 1). In 2017, a substantially higher number of trips were recorded compared to previous years due to the use of solar-panel loggers with a much longer battery life.

3. RESULTS

3.1. Behavioural classification

The 3-state HMM distinguished a state with very small step lengths (mean \pm SD: 75.9 ± 111.3 m) and no directionality ($h = 0$), a state with intermediate step lengths (944.7 ± 758.4 m) and weak directionality ($h = 0.43$) and a state with long step lengths (2746.1 ± 993.1 m) and strong directionality ($h = 5.71$) (Fig. 1). We interpret these as resting, foraging and in transit, respectively. Overall, 21 % of the locations were

Table 1. Sample size of tagged Sandwich terns per year and logger type (solar-powered or non-solar) for data used for the hidden Markov model (HMM) (all data but excluding parts venturing north of the 3D water movement and water quality modelling [TRIWAQ] area) and for the consistency analysis (only complete trips)

Year	Solar	HMM			Consistency analysis		
		No. of individuals	No. of trips	No. of positions	No. of individuals	No. of trips	No. of positions
2012	No	5	18	329	1	1	8
2013	No	3	23	1060	2	4	129
2014	No	7	30	629	5	12	269
2015	No	5	35	1166	5	8	302
2017	No	6	23	1862	4	8	384
2017	Yes	2	156	8304	2	140	6269
Totals		28	288	13918	19	173	7361

categorized as resting, 32% as foraging and 47% as in transit. Tagged Sandwich terns foraged in a large area around the colony during the breeding season. Most foraging occurred north of the colony, both nearshore as well as more than 30 km offshore (Fig. 2).

3.2. Environmental covariates affecting transition to and from foraging

Out of 512 models considered, 7 had $\Delta AIC < 2$ (Table 2). Allowing 2 or 3 ‘mixtures’ of transition probabilities in the top-ranking model reduced model fit ($\Delta AIC = 26$ and 52 , respectively). Therefore, we present parameter estimates for models without additional mixtures. From the 7 models with $\Delta AIC < 2$, all

included median grain size of the sediment, salinity and wave period as covariates on the transition probabilities (Fig. 3). The top-ranking model as well as 3 lower ranked models also included water depth. Cloud cover, wind speed and current speed were included in 3, 2 and 1 model, respectively. Air and water temperature were not included in any model with $\Delta AIC < 2$.

Focusing on the top-ranking model shows that Sandwich terns were more likely to switch from transit flight to foraging over coarser sediments (Figs. 3 & 4). Likewise, shallower water depths, lower salinity waters and shorter waves increased the likelihood of starting foraging behaviour, but the overlap of their 95% confidence intervals of odd ratios with 1 indicates only a weak response.

Birds were more likely to stop foraging and switch to transit flights over finer sediments, in deeper waters, in waters with lower salinity and with shorter waves (Figs. 3 & 4). In addition, they were more likely to switch to transit flights over deeper waters, but this parameter had a 95% confidence interval of odd ratios overlapping with 1, indicating a weak effect.

Birds were more likely to continue foraging over coarser sediments, whereas the probability of staying in the transit state decreased over those sediment types (Fig. 4). Birds were also more likely to continue foraging in areas with higher salinity, shallower waters and when wave periods were longer (Fig. 4).

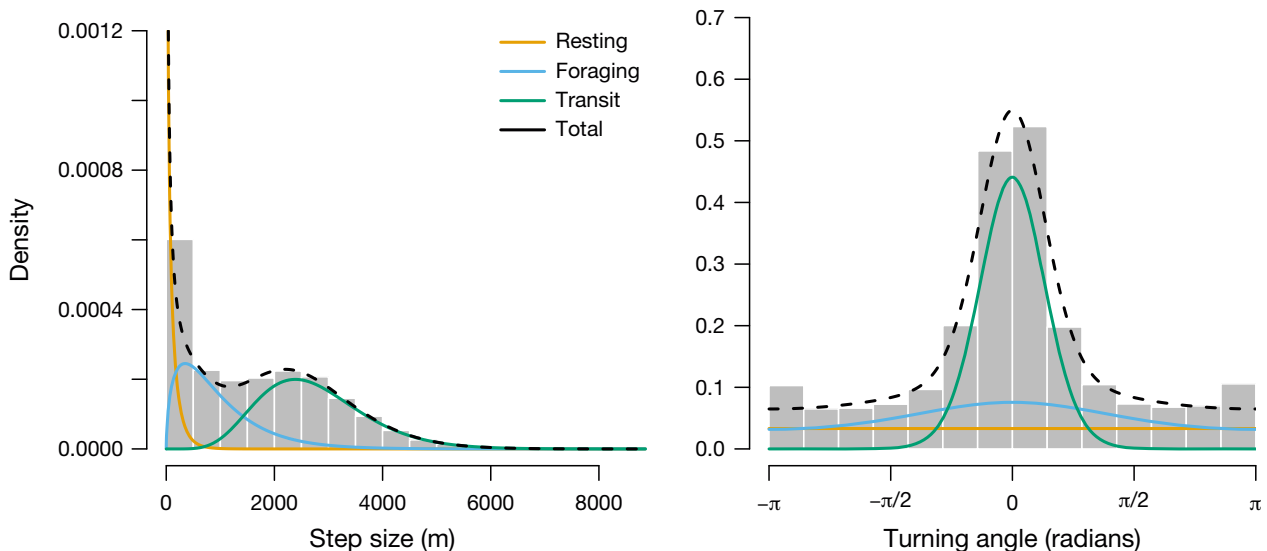


Fig. 1. Distribution of step lengths (left) and turning angle (right) per recognized behavioural state (resting, foraging, transit) of Sandwich terns as determined by the outcome of the hidden Markov model

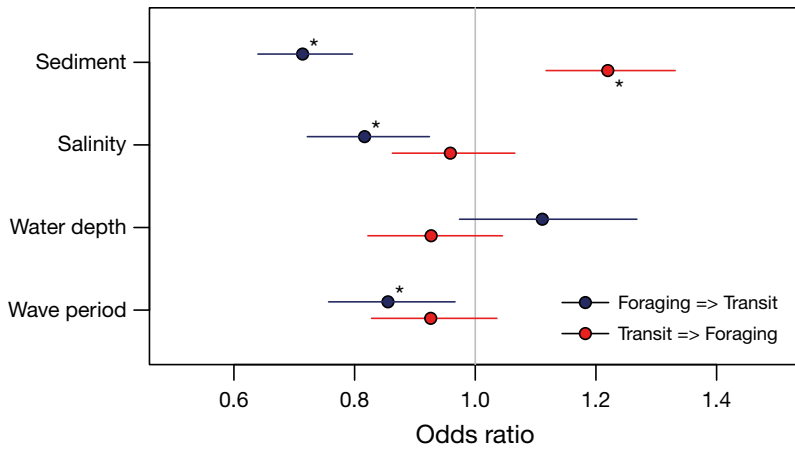


Fig. 3. Parameter estimates for probability transitions from the top-ranking model, with estimates ranked by their value for the transition of Sandwich terns from transit to foraging. Note that values further away from 1 have the largest effect size, with positive values indicating a positive relationship with the probability to switch behaviour, and that covariates have been standardized. Error bars: 95% CI; asterisks: 95% CIs do not overlap with 1. All variables were standardized

trips closer in time being slightly more similar than trips with longer time gaps.

The main driver of foraging behaviour in seabirds is the availability of prey. The main prey of Sandwich terns are forage fish in the upper 1.5–2.0 m layer of the water column. In the absence of real-time measurements of forage fish availability, proxies for prey fish availability were included in our model. One of these proxies is sediment grain size, which is linked to the presence of sandeels (Wright et al. 2000, Holland et al. 2005, Tien et al. 2017, Langton et al. 2021), an important prey type for Sandwich terns throughout the breeding season (Stienen et al. 2000, Courtenis et al. 2017) and also for many other seabirds in the North Sea (e.g. Furness 2002).

given the stronger effects of static rather than dynamic variables on foraging behaviour, terns were not more consistent or explorative between trips in the same phase of the tidal cycle or the time of day. However, there was some seasonal consistency, with

The sandeels' presence in the water column has a diurnal cycle. Sandeels are visual feeders that feed in the water column during the day and are mostly buried at night (Robards et al. 2002), when they associate with relatively coarse, sandy sediments (Wright

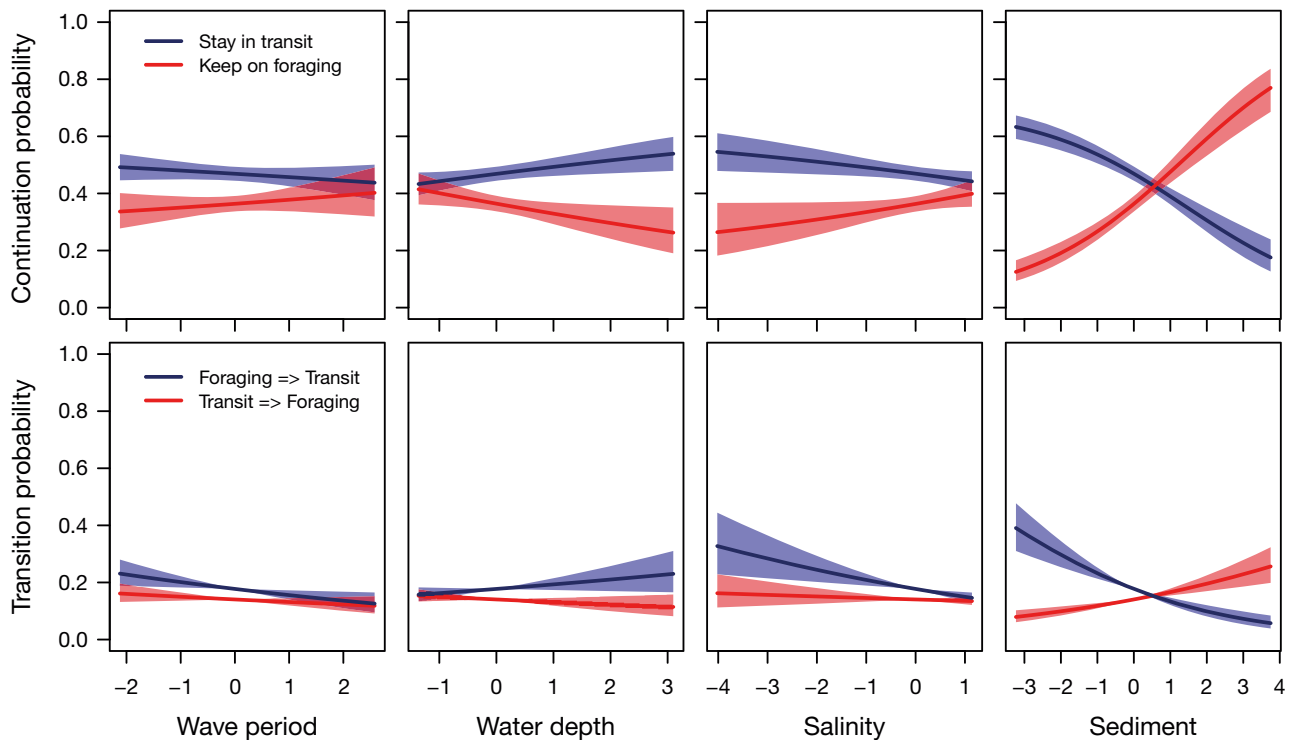


Fig. 4. Probability of Sandwich terns staying in the same state (continuation probability, upper panels) or switching to another state (transition probabilities, lower panels) for all variables retained in the top-ranking model. Shading represents the 95% CI around the prediction. All variables were standardized

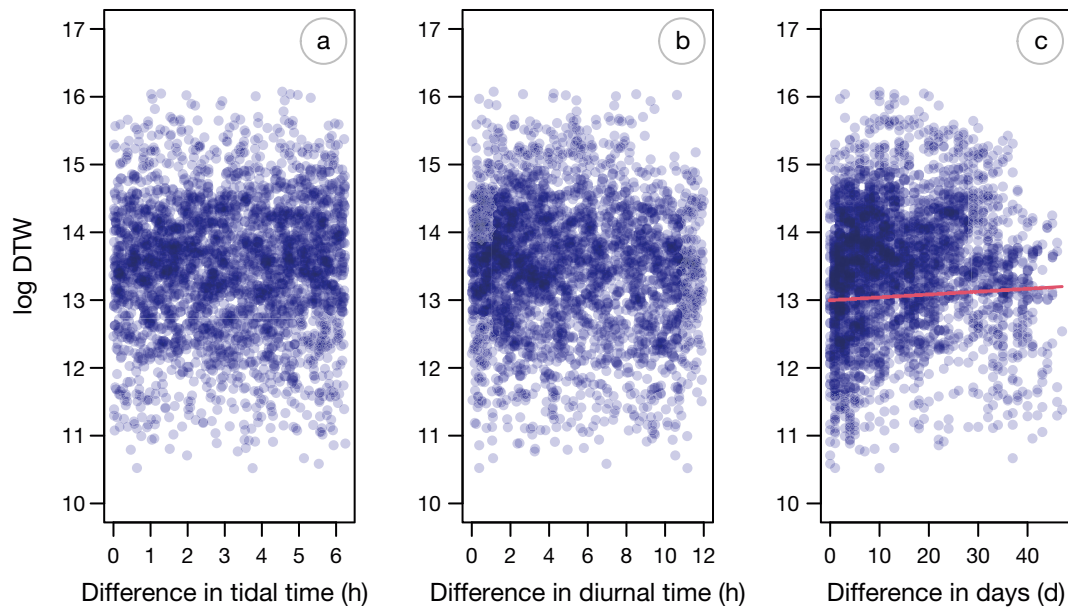


Fig. 5. Dynamic time warping (DTW) between 2 trips of the same individual Sandwich tern as a function of the difference in (a) hours to high tide, (b) time since sunrise and (c) day of year. Only the difference in day of year was retained in the top-ranking model, indicating that terns were not more consistent when trips were carried out during the same phase of the tidal cycle or the day and that trips close in time in the season were slightly more similar

Table 3. Comparison of models using dynamic time warping (log DTW) based on Watanabe-Akaike Information Criterion (WAIC)

Model covariates	Δ WAIC
~ Date	0.0
~ Tide + date	2.2
~ Tide + sunrise + date	4.2
~ 1	5.4
~ Tide	5.9
~ Sunrise	6.6
~ Tide + sunrise	11.5
~ Sunrise + date	15.0

et al. 2000, Holland et al. 2005, Tien et al. 2017, Langton et al. 2021). Higher abundance of sandeels over coarser sediments therefore likely explains the higher probability of Sandwich terns foraging over coarser sediments. Since sandeels form the staple diet of many seabird species in the North Sea, it is expected that many more seabird species in Western Europe target areas with coarser sediments.

Another proxy for prey distribution is the salinity level of the sea, which is linked to the presence (e.g. van der Kooij et al. 2008, Tien et al. 2017) as well as growth rates and survival of sandeels (e.g. Bonisławska et al. 2014). Like sediment grain size, salinity also showed spatial variation in our study area, mainly related to river run-off. Our results showed that terns

had a higher switch probability from foraging to transit flights over areas with lower salinity levels and switched to foraging over areas with higher salinity levels (possibly linked to higher sandeel abundance) in waters with higher salinity levels in our study area (Tien et al. 2017).

In addition to sandeels, other important prey of Sandwich terns are herring and sprat (Clupeidae). Whereas sandeels are available and captured by Sandwich terns throughout the breeding season, herring and sprat of the appropriate size are only available later in the breeding season, with variation in timing among years (Postuma et al. 1965). The seasonal availability pattern of herring and sprat is reflected in the adult and chick-feeding diets found in our study colony (Courstens et al. 2017, Fijn et al. 2018). Although herring and sprat may target food sources occurring on or near specific seafloor habitat types, their association with sediment type is unlikely to be as strong as for sandeels, which require a specific grain size to bury at night (Holland et al. 2005, Tien et al. 2017). Higher salinity levels, on the other hand, were previously found to predict herring distribution (e.g. Marshall & Elliott 1998), and the growth of these species was linked to specific (higher) salinity levels (e.g. Casini et al. 2010). This preference for higher salinity might explain the higher probability of Sandwich terns switching to foraging over areas with higher salinity levels.

Table 4. Qualitative variability of environmental conditions at temporal (seasonal, day-to-day, diurnal) and spatial (tidal, spatial) scales, categorized as strong variation (Y), some variation (Y/N) or no variation (N). Variables are ordered relative to their effect size in the top-ranking model, thus when the odds ratio is further from 1. NS: not significant

Variable	Seasonal	Day-to-day	Diurnal	Tidal	Spatial	Transition probability transit \geq foraging (odds ratio)
Median grain size	N	N	N	N	Y	1.22
Wave period	N	N	Y	N	Y	0.93
Water depth	N	N	N	Y	Y	0.93
Salinity	N	N	N	Y/N	Y	0.96
Current speed	N	N	N	Y	Y	NS
Water temperature	Y	N	N	N	Y/N	NS
Air temperature	Y	Y	N	N	N	NS
Wind speed	N	Y	N	N	N	NS
Cloud cover	N	Y	Y/N	N	N	NS

Other important drivers of foraging behaviour in seabirds are factors affecting prey capture efficiency. These variables are often related to weather conditions. Weather variables retained in competing models mainly vary daily and had smaller effects on the probability for terns to switch to foraging. Wave period was one of the covariates that influenced the transition probability in all 7 competing models, with terns being more likely to start foraging when waves were spaced longer. In several lower ranking models, weather variables such as (higher) cloud cover and (lower) wind speed were also included. Although wave period, cloud cover and wind speed did not show strong spatial patterns within the foraging range, previous studies have shown that these factors can affect the foraging efficacy of coastal seabirds (see Spear & Ainley 1997, Collins et al. 2020, De Pascalis et al. 2022 for the effect of wind on seabirds; Dehnhard et al. 2013, Lieber et al. 2019 for waves). Conceivably, cloud cover may increase the depths to which terns can detect prey under the water surface, as direct sunlight may cause reflection at the water surface. A similar relationship related to visibility of fish exists between foraging behaviour and wind speed, although this parameter was only significant in lower ranked models. Seabirds that use only flapping flight modes but no gliding generally expend more energy in stronger winds (Gabrielsen et al. 1987, Christensen-Dalsgaard et al. 2018, Lane et al. 2019), which may explain why birds would spend more time foraging in stronger winds. In addition, foraging efficiency may be lower in stronger winds (Stienen et al. 2000) due to difficulties in locating and relocating prey fish because of white wave caps and irregularity of the water surface. A more detailed study of the response of Sandwich terns to wind conditions may reveal whether wind conditions affect

trip characteristics (in line with Collins et al. 2020), such as the total duration and where and when foraging takes place.

Water depth also seems to play a small role in the transition between transit and foraging. Why water depth would drive foraging behaviour of Sandwich terns is not clear. Shallower waters might help small fish avoid predators such as larger fish, seals and harbour porpoises in deeper water (Munsch et al. 2016) and might also force prey fish closer to the surface, thus leading to their increased abundance and catchability in shallower water. Shallower water is also warmer, which could enhance algae growth, the primary food source for several fish species (Blaxter 1992), leading to higher growth rates (Smigielski et al. 1984) and stocks (Robards et al. 2002) of sandeel. However, Tien et al. (2017) found no evidence for higher temperatures being related to sandeel distribution in the Voordelta. In herring, and probably also sprat, growth rates increase with temperature (Høie et al. 1999, Brunel & Dickey-Collas 2010), and warmer water is preferred by their larvae (Batty et al. 1993). The higher probability of transition between transit and foraging in shallower water by Sandwich terns potentially reflects their foraging behaviour on herring-type prey rather than on sandeels.

Unfortunately, water transparency data were not available for our study area. Seabirds show variable preferences for turbidity levels (e.g. Shealer 2002). Clear waters are preferred by some visual hunters (e.g. Kowalczyk et al. 2015), although increased visibility may improve the chance for fish to escape (e.g. Sohel & Lindström 2015). Other visual foragers, and terns in particular, are often found in more turbid waters (e.g. Haney & Stone 1988, Henkel 2006) despite the reduction in visibility these conditions bring. Baptist & Leopold (2010) showed that Sand-

wich terns select an optimum level of water transparency for foraging between clear and turbid waters. Expanding our models with turbidity levels would probably improve the model fits and prove to be a strong predictor of Sandwich tern foraging.

Here, environmental covariates were modelled as linear effects on transition probabilities between transit flights and foraging, with no interactions between variables. However, the relationship between behaviour and environmental conditions may be non-linear, which may explain some apparently contradicting results. For example, transition to foraging was more likely over coarser sediment but also at shallower depths, whereas coarser sediments more commonly occur in deeper waters. It is possible that the linear effects of sediment grain size and water depths capture different parts of the non-linear relationship, whereby Sandwich terns target a specific grain size at an intermediate water depth.

There was considerable overlap between the step lengths and turning angle distributions of foraging and transit flights, implying uncertainty in our Viterbi-based classifications of behaviour. Based on visual inspection of the classifications along tracks, most Viterbi-based classifications agreed with our expectations. For example, foraging segments were concentrated at the far end of a foraging trip and clustered in particular areas across multiple foraging trips and individuals. In addition, the distribution of flight speed for foraging and transit as inferred by the HMM agreed with flight speeds based on an earlier manual classification using parts of the same data (Fijn & Gyimesi 2018). In some segments that were classified as foraging, birds travelled relatively slowly but with considerable directionality. Indeed, Sandwich terns often forage while following a straight flight path (thus with strong directionality), for example when foraging along the surf zone or an oceanic front (Cabot & Nisbet 2013). Behavioural classifications of Sandwich tern tracking data using HMMs can be improved by adding auxiliary biotelemetry data, such as dive activity or accelerometer data (McClintock & Michelot 2018).

Our tracked Sandwich terns showed a consistent preference for the northern part of their home range for foraging (Fig. 2). Interestingly, the southern part of their home range has much lower densities of *Ammodytes marinus* compared to the northern part, but *A. tobianus* is present in similar densities in both areas (Tien et al. 2017). This might suggest *A. marinus* to be the preferred prey item for Sandwich terns. Alternatively, the southern area may offer less suitable abiotic conditions in terms of water trans-

parency or wave and current activity, as this is a more sheltered area behind large coastal sand banks. In the north, the presence of a persistent river plume (Nieuwe Waterweg) might cause frontal areas and other ephemeral hydrographic phenomena, which might be clues for foraging but were not picked up by our models. Finally, Sandwich terns may also move north to avoid interspecific competition from Sandwich terns from more southerly located colonies (Fig. 2), as observed in many other seabirds (e.g. González-Solís et al. 2000, Wakefield et al. 2013, Robertson et al. 2014, Austin et al. 2021).

Given that the strongest effect on foraging behaviour was found to be a (largely) static rather than dynamic variable, Sandwich terns may be expected to target the same sites during different foraging trips, with little variation in the degree of consistency across tidal, diurnal or seasonal cycles. Our results suggest that trips close in time within the season were slightly more similar than trips with a larger time gap, but this effect was weak. The low spatial consistency contrasts with findings for other seabird species that mainly rely on static habitat features, such as coastal-dwelling great cormorants *Phalacrocorax carbo* (Grémillet et al. 1999, Potier et al. 2015) that were found to visit the same sites trip after trip, but is in line with studies indicating variability of habitats does not always drive individual consistency (Granadeiro et al. 2014, Shoji et al. 2016). The low foraging-site fidelity of Sandwich terns suggests that they target broad areas that are suitable for prey and where ephemeral conditions can occur that cause prey to be available to terns. In our study, we were not able to identify such ephemeral foraging conditions. Future studies, deploying tracking devices that record behaviour at very high temporal resolution and in 3 dimensions (e.g. with accelerometers), could provide more detailed behavioural data, but a continuing difficulty will be to measure the relevant environmental variables that capture foraging opportunities for feeding seabirds.

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