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Environmental heterogeneity amplifies behavioural response to a temporal cycle

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Resource acquisition is integral to maximise fitness, however in many ecosystems this requires adaptation to resource abundance and distributions that seldom stay constant. For predators, prey availability can vary at fine spatial and temporal scales as a result of changes in the physical environment, and therefore selection should favour individuals that can adapt their foraging behaviour accordingly. The tidal cycle is a short, yet predictable, temporal cycle, which can influence prey availability at temporal scales relevant to movement decisions. Here, we ask whether black-legged kittiwakes *Rissa tridactyla* can adjust their foraging habitat selection according to the tidal cycle using GPS tracking studies at three sites of differing environmental heterogeneity. We used a hidden Markov model to classify kittiwake behaviour, and analysed habitat selection during foraging. As expected for a central-place forager, we found that kittiwakes preferred to forage nearer to the breeding colony. However, we also show that habitat selection changed over the 12.4-h tidal cycle, most likely because of changes in resource availability. Furthermore, we observed that environmental heterogeneity was associated with amplified changes in kittiwake habitat selection over the tidal cycle, potentially because environmental heterogeneity drives greater resource variation. Both predictable cycles and environmental heterogeneity are ubiquitous. Our results therefore suggest that, together, predictable cycles and environmental heterogeneity may shape predator behaviour across ecosystems.

Keywords: foraging behaviour, habitat selection, predictability, seabird, tide

Introduction

The need to acquire resources to survive and reproduce is fundamental to all animals. Searching for resources is costly, and therefore selection favours individuals that can maximise foraging efficiency by matching the distribution of their target resources (Stephens and Krebs 1986). When prey distribution is stable, consistent area use is adaptive (Weimerskirch et al. 2005). However, resources typically vary both in space and time (Weimerskirch et al. 2005). For example, the physical environment can

concentrate prey into patches (Genin 2004) and predictable cycles can alter prey abundance (Yamamoto et al. 2008, Brierley 2014). Furthermore, temporal changes in resource distribution may be explicitly linked to the structure of the physical landscape (Boulinier et al. 2001). In physically less variable environments, a temporal change may have a spatially uniform effect on resources. In contrast, where physical features enhance or interrupt temporal changes, the response of resources will vary in space (Benjamins et al. 2015). In combination, both temporal and spatial variation in the physical environment can shape when and where animals can find resources. An animal's ability to learn and adapt to such changes will offer a vital opportunity to increase fitness, and hence should be under selection.

Adaptive foraging behaviour is a key link between environmental variability, resources and fitness (Matthiopoulos et al. 2015). Animals can adapt to resource differences by using a profitable subset of habitat types within the landscape available to them. Habitat preferences have been widely demonstrated for spatial landscape features (Leclerc et al. 2016, Christensen-Dalsgaard et al. 2017), and can change over time in response to factors such as predictable, long-term, seasonal resource cycles (Guyot et al. 2017) or changing predation risk (Godvik et al. 2009, Lone et al. 2017). However, while resources are known to change at very fine temporal scales (Zamon 2003), associated fine-scale changes in habitat selection, and whether environmental heterogeneity can influence behavioural responses, are less understood. Such adaptive responses to predictable resource changes would increase foraging efficiency, and therefore likely enhance an individual's fitness.

Resource distribution in the marine environment is both spatially and temporally variable (Pinaud et al. 2005, Weimerskirch et al. 2005), and so marine ecosystems are a model system to study changes in habitat selection with temporal cycles and environmental heterogeneity. In coastal seas, the tidal cycle has an important influence on ecosystem dynamics (Embling et al. 2012, Cox et al. 2018). The tidal coupling hypothesis (Zamon 2003) suggests that interactions between tidal currents and variation in bathymetry (the depths of the sea floor) create predictable changes in resource availability. It considers that physical features, such as islands or channels, interrupt and change the flow of currents, which in turn drives predictable changes in zooplankton abundance and distribution (Johnston and Read 2007, Benjamins et al. 2015). These changes can increase prey accessibility and vulnerability, and hence marine predators are often found foraging in areas of high tidal activity (Johnston et al. 2005, Bailey and Thompson 2010). For example, in tidal channels, studies have observed that tidal cycles lead to fluctuating numbers of diving seabirds (Holm and Burger 2002) and marine mammals (Johnston et al. 2005, Hastie et al. 2016). There is also evidence that seabird numbers fluctuate with the tide further offshore (Zamon 2003, Embling et al. 2012, Cox et al. 2013), although the nature of these relationships varies between locations (Zamon 2003, Embling et al. 2012,

Cox et al. 2013). Such geographic differences in behavioural responses to the tidal cycle may arise because of location-specific interactions between bathymetry and tidal currents (Scott et al. 2013, Waggitt et al. 2016, Cox et al. 2018). The surrounding environment may also play a key role in shaping behavioural responses, and therefore warrants further study (Benjamins et al. 2015).

In this study, we explore changes in foraging habitat preferences of black-legged kittiwakes (*Rissa tridactyla*, hereafter 'kittiwakes') over the predictable semi-diurnal (~12.4-h) tidal cycle. Kittiwakes feed at the surface, predominately on shoaling fish such as lesser sandeel, *Ammodytes marinus* (Daunt et al. 2002). Breeding kittiwakes are constrained in the timing of their foraging trips by the behaviour of their partner (Coulson and Wooller 1984). Furthermore, whilst provisioning chicks, kittiwakes are relatively short-ranging central-place foragers (Daunt et al. 2002), and are thus constrained to the physical environment surrounding their colony. As with many other central place foragers, kittiwakes live within finely balanced energy budgets (Collins et al. 2016). As such, distance to the colony is known to be a primary driver of foraging behaviour, as animals seek to minimise energy expenditure from flight costs during travel to foraging areas (Chivers et al. 2013, Collins et al. 2016). A decision, therefore, to forage further from the colony may signify an important adaptation to maximise foraging gains.

In order to study foraging adaptations of kittiwakes to the physical environment and the tidal cycle, we first consider behaviour in relation to distance to the colony, and then explore fine-scale adaptations of habitat selection to the environment and temporal changes. We predict that kittiwakes will preferentially remain close to the colony, and therefore will selectively forage in water depths that are found close to the colony. Because tidal currents interact with bathymetry to change prey availability to predators, we expect that preference for different water depths within the bathymetric landscape will change over the 12.4 h tidal cycle. Furthermore, in more heterogeneous environments where changes in bathymetry are more common and tidal changes are more pronounced, we hypothesise that kittiwakes will adjust their habitat selection more over the tidal cycle than in homogeneous environments.

Material and methods

GPS tracking

To determine fine-scale movement behaviour of kittiwakes, we attached GPS loggers (weighing 15.3 g in 2010 and 2011; and subsequently 10.3 g with modified battery in 2015–2017) to the back feathers between the wings using 3 g of waterproof tape. We deployed loggers at three UK kittiwake colonies (Fig. 1a): Puffin Island (NW Wales; 53°32′N, 4°03′W); Skomer Island (SW Wales; 51°74′N, 5°30′W); and Rathlin Island (Northern Ireland; 55°30′N, 6°27′W),

during chick rearing (June–July) and retrieved them after an average of 2.7 ± 1.25 days ($\pm$ SD). GPS tracks were obtained for a total of 457 trips from 80 individuals: 341 trips from 49 individuals at Puffin Island (14 individuals in 2010, 20 in 2011, 9 in 2015 and 10 in 2016), 33 trips from 14 individuals at Skomer Island (11 individuals in 2016 and 6 in 2017) and 83 trips from 17 individuals at Rathlin Island (2017 only). At Puffin Island, two individuals were tracked in two different study years, and one individual was tracked in three different study years. At Skomer Island, three birds were tracked in both study years. Full sample sizes are given in the Supplementary material Appendix 1 Table A1. The loggers recorded a GPS location every two minutes, between the hours of 03:00 and 23:00 to reduce battery consumption overnight when kittiwakes exhibit minimal foraging activity (Daunt et al. 2002). GPS data were not interpolated. To eliminate departures from the colony because of disturbance (Collins et al. 2016, Warwick-Evans et al. 2016b), we excluded points closer than 300 m to the colony, and attributed sequential points to a foraging trip if the total trip duration was over 14 min (based on a frequency distribution of trip duration; Warwick-Evans et al. 2016b). Hereafter we refer to fixes recorded by GPS loggers as locations used by kittiwakes. All data manipulation and analyses were conducted in R ver. 3.2.2 (<www.r-project.org>).

Environmental data

Bathymetry data were collated from the UK Hydrographic Office (UKHO) Data Archive Centre for bathymetric surveys and integrated with the General Bathymetric Chart of the Oceans (GEBCO). UKHO data contains public sector information, available under the Open Government Licence as part of the INSPIRE initiative. UKHO data, collected from boat surveys, covered a subset of the study areas at between 2 and 4 m resolution. Bathymetry from UKHO data were available for 66.8% of the locations used by kittiwakes. Depths for the remaining locations were extracted from GEBCO data, which is a global bathymetric grid with 30″ resolution (approximately 1 km), updated in 2014. However, because both UKHO and GEBCO bathymetry follow a relatively coarse grid for the coastline, 7% of locations used by kittiwakes fell outside the gridded bathymetry data. For these locations, we used the mean bathymetry from all GEBCO grid cells within a 1.1 km radius. This buffer slightly exceeds the resolution of GEBCO data and was sufficient to capture bathymetry data for all locations used by kittiwakes. Percentage coverage of each type of bathymetry data at each colony are given in the Supplementary material Appendix 1 Fig. A1.

Times during the tidal cycle for each kittiwake location were generated using POLTIPS tidal software (v.3.9.0/16; National Oceanography Centre UK, 2013). The Irish Sea and surrounding areas (Fig. 1) are strongly influenced by tidal processes, having significant tidal ranges (exceeding 10 m in the Bristol Channel) and extreme tidal races (exceeding 2.5 m s^{-1} around NW Anglesey) (Polton et al. (2011), see also for a dynamical review of the region). Data were extracted from the nearest secondary port to the study colony (Trwyn Dinmor 1 km from Puffin Island, Skomer Island for Skomer Island, and Ballycastle Bay 10 km from Rathlin Island). Tide times may vary across the kittiwake foraging range by up to 20 min at Puffin Island, and up to an hour at Skomer Island. At Rathlin Island tide times may be more variable, however there are few nearby secondary ports for tidal calculations and tidal amplitudes are small. We therefore derived tide times at all colonies from a single location to maintain consistency between study sites. We split the ~12.4-h tidal cycle into four sections relative to the time of local high water, since flow characteristics are known to affect prey behaviour and distribution (Zamon 2002, Embling et al. 2012): 1) slack low: >5 h either side of high water to correspond to low flow rate either side of low tide; 2) flood: between 5 and 1 h before high water, high flow rate during the rising tide; 3) slack high: 1 h either side of high water, low flow rate around high tide; and 4) ebb: between 1 and 5 h after high water, high flow rate during the falling tide. Each kittiwake location was assigned to a section of the tidal cycle according to the time before or after high water that the GPS fix was recorded.

Assessing environmental heterogeneity of colonies

To investigate how the degree of environmental heterogeneity influenced kittiwake foraging behaviour, we compared the physical environment surrounding each breeding colony by characterising depth and tidal regime within the maximum foraging range of kittiwakes, defined as the maximum linear distance from each colony from kittiwake tracking data. To do this, following Verney et al. (2006), we compared bathymetry and tidal shear stress. Tidal shear stress is a measure of the amount of turbulence caused by the friction between tidal flow and the seafloor, and is used as a proxy for the extent to which tidal flow alters the foraging environment over the tidal cycle. Tidal shear stress is simulated numerically at 1.8 km resolution over the North West European shelf (Guihou et al. 2018), further details given in Supplementary materials Appendix 2. We used ANOVA and post hoc Tukey tests to determine whether the environment differed between colonies. We compared mean values, standard deviation and the range of values as an indication of spatial environmental heterogeneity at each colony.

Behavioural classification

To study habitat selection whilst foraging, we used a hidden Markov model to classify behaviour from GPS tracking data using the package moveHMM (Michelot et al. 2016). Behaviour of an individual during trips away from the colony was classified as either foraging, resting or transiting (Chivers et al. 2012) based on distributions of step lengths and turning angles between consecutive locations. Standard deviation of time steps of the data are small (around 2 s), and so we assume that our time steps are sufficiently regular for
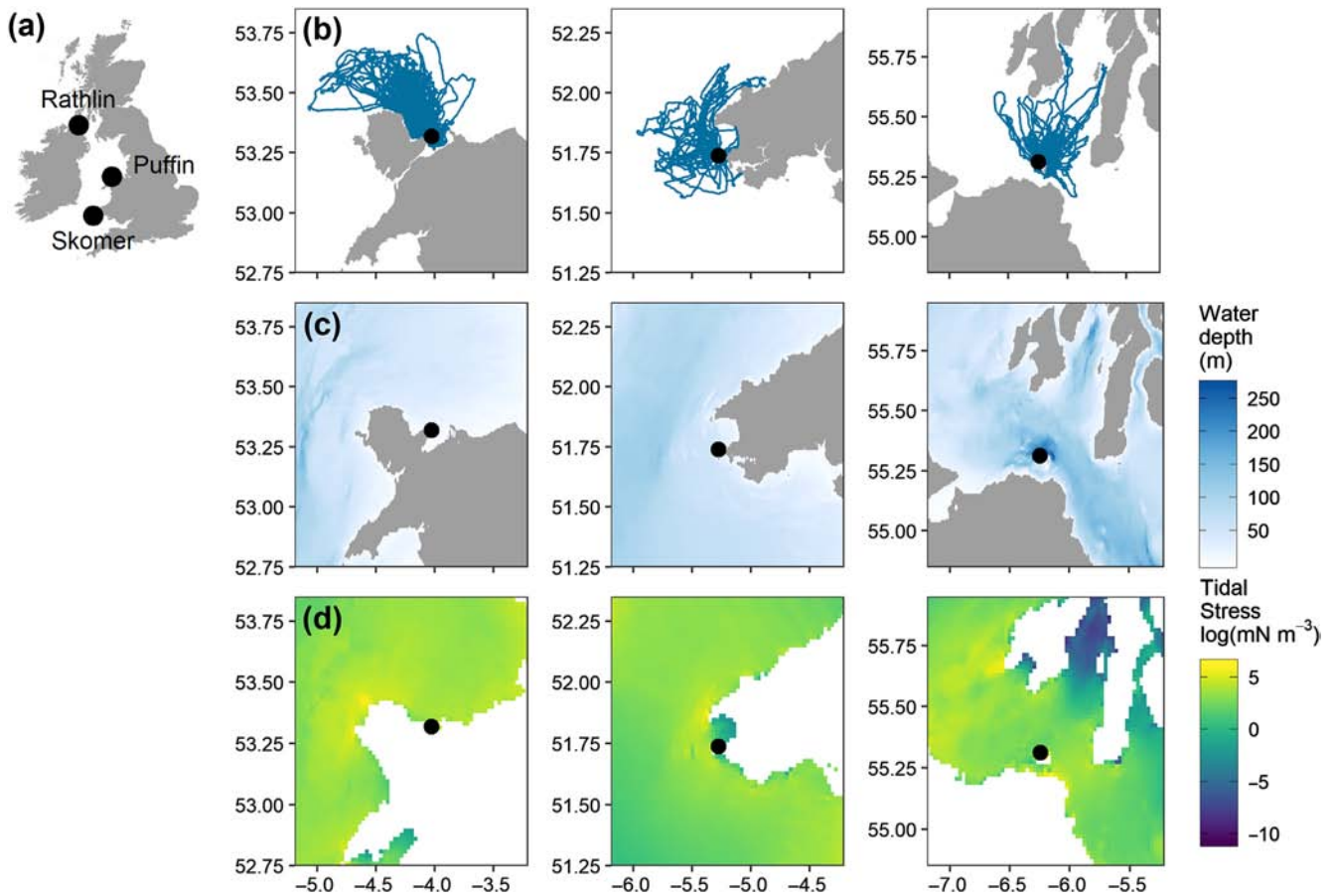
Figure 1. Colony locations around the UK (a) and areas around Puffin Island (left), Skomer Island (middle) and Rathlin Island (right) showing (b): GPS tracks of kittiwakes (Puffin island: 2010–2011 and 2015–2016, n = 49; Skomer Island: 2016–2017, n = 14; and Rathlin Island: 2017, n = 17), (c) water depths and (d) depth-standardised tidal shear stress. In all plots, the study kittiwake colony is marked with a point.

this approach, which also allowed us to model real locations rather than interpolated locations in the habitat selection analysis described below. We used a gamma distribution to describe step lengths and a von Mises distribution to describe turning angles. We used the Viterbi algorithm to estimate the most likely sequence of movement states based on the fitted hidden Markov model (Supplementary material Appendix 3). Hidden Markov models use prior estimates of step length and turning angle distributions, and therefore we ran 25 models with different distribution starting parameters to test model sensitivity (Grecian et al. 2018).

Habitat selection analysis

To determine whether kittiwake foraging behaviour is influenced by a predictable cycle and the degree of environmental heterogeneity, we tested whether spatial habitat selection by kittiwakes varied temporally over the tidal cycle, and between study colonies with different degrees of environmental heterogeneity. Firstly, because of the importance of colony location to foraging behaviour of breeding kittiwakes (Chivers et al. 2013), we considered differences in habitat selection by

distance to the colony. Secondly, because the tidal coupling hypothesis suggests that tidal currents and bathymetry interact to change the foraging environment over the tidal cycle, we considered differences in habitat selection of water depth.

Habitat selection functions were performed using generalised linear mixed effects models to compare the habitat used by the birds with the habitat available to them (Aarts et al. 2012). A dataset of available habitat was generated for 10 random geographic points (Northrup et al. 2013) per foraging location used by kittiwakes from within the foraging range of the colony in the given study year (Christensen-Dalsgaard et al. 2017). Random points were selected using the sample Random function of the R package raster (Hijmans and Jacob 2016). Habitat use (binomial response variable: y; available = 0 or used = 1) was modelled in response to three explanatory variables: 1) the physical environment (either colony distance or depth in two separate models, standardised to mean = 0, sd = 1), 2) tidal state (four-level factor), and 3) colony (three-level factor). Colony distance or depth were included in a three-way interaction with tidal state and colony to explore how the degree of environmental heterogeneity influences the interaction between constant

landscape characteristics and temporal cycles. Models were implemented using a binomial error structure with a logit link using the glmer function of the R package lme4 (Bates et al. 2015). We selected the random effects structure based on pseudo-replication in the sampling design, in all cases including trip ID nested within individual ID as random intercepts in the model. We also included a colony-specific factor for year as a random effect to allow for year differences specific to each colony. We selected the most suitable fixed effects structure based on AIC values in backward stepwise selection, and checked model fit by calculating the area under the receiving operator characteristic curve (AUC) (Zweig and Campbell 1993), predictive power, sensitivity and specificity (Warwick-Evans et al. 2016a) (Supplementary material Appendix 4 Table A4.3). Testing by inspection of Moran's I of model residuals at each colony revealed that there was no influence of spatial autocorrelation in any of our findings (Moran's $I < 1$, $p = 1$) (Diniz-Filho et al. 2003). Variance explained, R^2, was calculated using the sem.model. fits function of the R package piecewiseSEM (Lefcheck 2016) following methods in Nakagawa and Schielzeth (2013). To ensure accurate characterisation of habitat preference of kittiwakes, we assessed model sensitivity to the maximum foraging range used to select available habitat, and including all GPS locations, rather than just foraging points (Northrup et al. 2013). Results of sensitivity analyses (Supplementary material Appendix 3) are consistent with those presented in the results, and thus we believe our analyses are robust to available habitat selection methods.

In addition to the two models described above, to further understand how the degree of environmental heterogeneity can change the effect of a predictable cycle on behaviour, we ran habitat selection models at each colony separately. We explored differences between colonies in the variance explained by the two-way interaction of tide and the environmental variable in question (distance to the colony or depth) to determine the effect of the tidal cycle on kittiwake spatial behaviour. In addition, we extracted parameter estimates for habitat selection at different tidal states to compare the probability of habitat use at different tidal states at each colony. Models were structured as above, however without colony as a factor in the fixed effects structure.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1447866> (Trevail et al. 2018).

Results

Foraging trip metrics

Foraging trips from Puffin Island and Rathlin Island were comparable in mean duration, mean distance travelled and mean maximum distance reached from the colony (Table 1, Fig. 1b). At Skomer Island, foraging trips were, on average, longer in duration, distance travelled, and reached furthest from the colony (Table 1, Fig. 1a). Summaries of trip durations and distances for each year at each colony are given in Supplementary material Appendix 1 Table A2. GPS tracking spanned across the spring-neap cycle at Puffin Island, and was between springs and neaps at both Skomer and Rathlin (Supplementary material Appendix 1 Fig. A2), thus reducing the potential influence of the spring-neap cycle on our findings.

Differences in proximal environment and heterogeneity between colonies

To assess the degree of local environmental heterogeneity, we compared local bathymetry (Fig. 1c) and tidal shear stress (Fig. 1d). Within the foraging range of GPS tracked kittiwakes, at Puffin Island bathymetry was shallower and more homogeneous (mean $\pm$ SD $= 35.9$ m $+ 20.9$) compared to Skomer Island (65.3 m $\pm$ 27.1) and Rathlin Island (76.5 m $\pm$ 42.4). Furthermore, at Puffin Island, tidal flow caused the least amount of change in the foraging environment over the tidal cycle (maximum shear stress $= 401$ mN m^{-3}), compared to Skomer Island (448 mN m^{-3}) and Rathlin Island (523 mN m^{-3}). At both Puffin Island and Skomer Island the water adjacent to the colony was shallow, whereas at Rathlin Island, the deepest waters within the foraging range (over 200 m) were found within 10 km of the colony (Fig. 1c). Based on the differences in bathymetry and tidal shear stress (further details in Supplementary material Appendix 2) we identified different degrees of environmental heterogeneity between the study colonies, both in terms of spatial (bathymetry) and temporal (tide) variability; Puffin Island: low heterogeneity, Skomer Island: medium heterogeneity and Rathlin Island: high heterogeneity.

Habitat selection

Habitat selection by distance to the colony and depth were analysed separately, and in both cases the most parsimonious models according to AIC values (Supplementary material

Table 1. Summary of kittiwake foraging trip characteristics at each colony over all study years (Puffin island: 2010–2011 and 2015–2016; Skomer Island: 2016–2017; and Rathlin Island: 2017). Full details of sample sizes and trip characteristics for each year are given in the Supplementary material Appendix 1.

Colony	Mean trip duration (h $\pm$ SE)	Mean total distance travelled (km $\pm$ SE)	Mean maximum distance from the colony (km $\pm$ SE)
Puffin	3.8 $\pm$ 0.3	39.4 $\pm$ 2.5	11.9 $\pm$ 0.7
Skomer	9.7 $\pm$ 1.5	90.0 $\pm$ 13.3	22.0 $\pm$ 2.6
Rathlin	3.4 $\pm$ 0.3	39.7 $\pm$ 3.7	13.5 $\pm$ 1.3

Table 2. Parameter estimates (slope ± 95% CI) for the most parsimonious model of kittiwake habitat selection by distance to the colony. All values are below zero (dashed line), indicating a general preference for remaining closer to the colony. Lower negative values, indicate stronger preference for habitat closer to the colony. Model is a generalised linear mixed effects model with a binomial response of habitat use (used = 1, available = 0), with year (specific to colony), BirdID and TripID included as random effects. Tidal states are defined as slack low: >5 h either side of high water; flood: 1–5 h before high water; slack high: 1 h either side of high water; and ebb: 1–5 h after high water. Environmental heterogeneity is low at Puffin Island, medium at Skomer Island and high at Rathlin Island.

Colony	Tidal state	Colony distance selection estimate (slope and 95% CI)	No. of individuals	No. of trips
Puffin	overall	−2.87 [−3.21, −2.55]	49	341
	slack low	−2.46 [−2.79, −2.12]	45	147
	flood	−2.64 [−2.97, −2.31]	49	206
	slack high	−3.75 [−4.08, −3.41]	46	141
	ebb	−2.84 [−3.18, −2.51]	49	215
Skomer	overall	−1.94 [−2.50, −1.39]	14	33
	slack low	−1.62 [−2.18, −1.07]	13	22
	flood	−2.46 [−3.02, −1.91]	14	30
	slack high	−1.84 [−2.40, −1.28]	13	20
	ebb	−1.65 [−2.21, −1.09]	14	22
Rathlin	overall	−3.41 [−4.07, −2.75]	17	83
	slack low	−8.60 [−9.61, −7.59]	15	28
	flood	−2.14 [−2.78, −1.49]	16	40
	slack high	−2.32 [−2.97, −1.67]	17	39
	ebb	−2.34 [−2.99, −1.69]	17	53

Odds ratio

Appendix 4 Table A4.1, A4.2) were the 'full models' that retained the three-way interaction between the environment variable in question (distance to the colony or depth), tidal state and colony. This means that habitat selection by kittiwakes was influenced by distance to the colony and local bathymetry, varied over the tidal cycle, and that the response to the tidal cycle was different between environments. Depth also influenced kittiwake habitat selection, which also varied according to the tidal cycle and with environmental heterogeneity. Model parameter estimates are given for habitat selection by colony distance in Table 2, and for habitat selection by depth in Table 3.

Distance to the colony was a significant driver of kittiwake foraging behaviour; the full model accounted for over two thirds of the total variance (marginal $R^2 = 65\%$). At all colonies, kittiwakes had higher probability of using habitat closer to the colony (Fig. 2). The probability of remaining closer to the colony was strongest at Rathlin Island (high heterogeneity) (parameter estimate on logit scale ± SE: $−3.41 ± 0.34$), weakest at Skomer Island (medium heterogeneity) ($−1.94 ± 0.28$) and intermediate at Puffin Island (low heterogeneity) ($−2.87 ± 0.17$).

Bathymetry preferences of kittiwakes corresponded to water depths close to the study colony (Fig. 3). The full model

Table 3. Parameter estimates (slope ± 95% CI) for the most parsimonious model of kittiwake habitat selection by depth, where values below zero (dashed line) indicate preference for shallower water, and values above zero indicate preference for deeper water.

| Colony	Tidal state	Depth selection estimate (slope and 95% CI)	No. of individuals	No. of trips
Puffin	overall	−11.28 [−11.41, −11.15]	49	341
	slack low	−10.24 [−10.48, −10.00]	45	147
	flood	−11.40 [−11.60, −11.21]	49	206
	slack high	−13.55 [−13.81, −13.29]	46	141
	ebb	−10.38 [−10.58, −10.19]	49	215
Skomer	overall	−6.70 [−6.91, −6.48]	14	33
	slack low	−4.90 [−5.18, −4.62]	13	22
	flood	−8.55 [−8.86, −8.23]	14	30
	slack high	−5.98 [−6.39, −5.57]	13	20
	ebb	−6.27 [−6.57, −5.96]	14	22
Rathlin	overall	2.90 [2.74, 3.06]	17	83
	slack low	3.62 [3.35, 3.90]	15	28
	flood	1.25 [1.06, 1.43]	16	40
	slack high	3.27 [3.07, 3.48]	17	39
	ebb	3.97 [3.79, 4.15]	17	53

Odds ratio
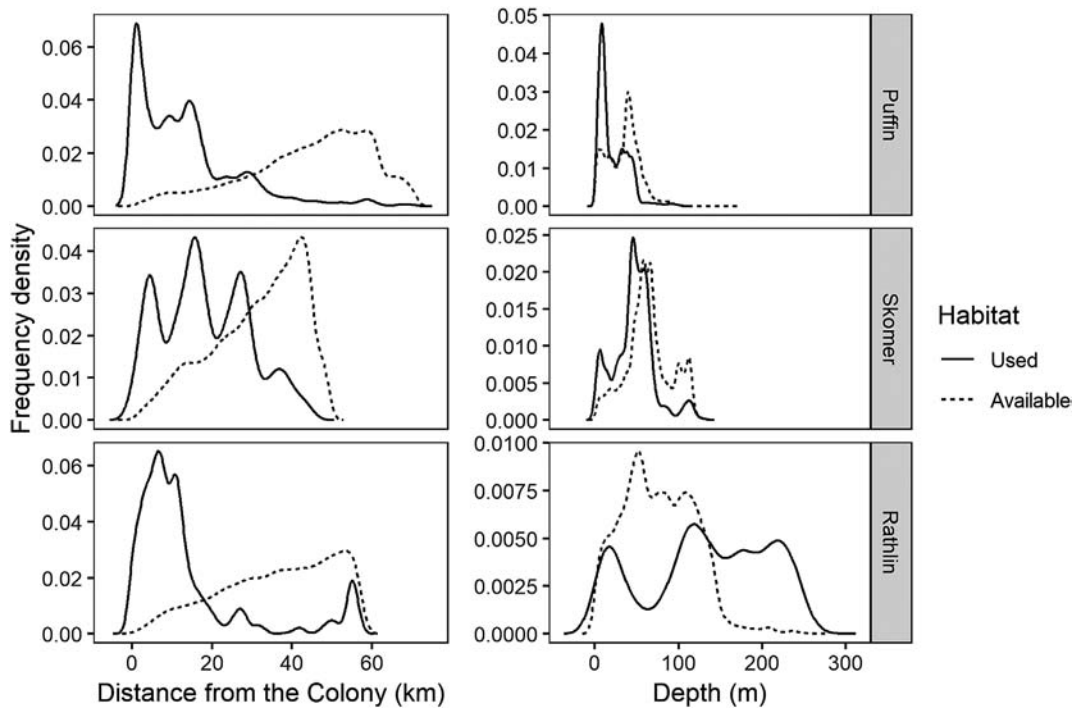
Figure 2. Density curves of available habitat (sampled for 10 random points per foraging GPS point) and habitat used by kittiwakes whilst foraging (GPS points classed as foraging from HMM model) with increasing distance from the colony (left) and water depths (right) at the three study colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Greater density of used than available habitat indicates selection of that particular habitat. At all colonies, habitat close to the colony was used at a greater frequency density than available, indicating preference for remaining close to the colony. At Puffin Island and Skomer Island, shallower waters were used at a greater frequency density than available, indicating preference for shallower waters, whereas at Rathlin Island, deeper waters were used at a greater frequency density than available, indicating preference for deeper waters.

showed that bathymetry affected kittiwake habitat choice (marginal $R^2 = 19.8\%$). However, as expected, this model explained less variance than the full model of habitat selection by colony distance. The effect of bathymetry on habitat selection was strongest at Puffin Island (low heterogeneity) (parameter estimate on logit scale $\pm$ SE: -11.28 ± 0.07), weakest at Rathlin Island (high heterogeneity) (2.90 ± 0.08) and intermediate at Skomer Island (medium heterogeneity) (-6.70 ± 0.11). At Puffin Island and Skomer Island, where bathymetry close to the colony was shallower (Fig. 1), kittiwakes had higher probability of using shallow water (Fig. 3), whereas at Rathlin Island, which was adjacent to very deep water (Fig. 1), kittiwakes had higher probability of using deeper water (Fig. 3).

Kittiwake habitat selection changed during the predictable 12.4-h tidal cycle (Table 2, 3), and the change in kittiwake habitat selection over the tidal cycle differed in magnitude between the colonies (Table 2, 3). The most parsimonious habitat selection models for each colony separately according to AIC values (Supplementary material Appendix 6 Table A6.3, A6.4) were the models including the two-way interaction between the environmental variable in question (distance to the colony or depth) and tidal state. Based on these models, the interaction between

tide and the environmental variable (distance to colony or depth) explained more additional variation in the model at Rathlin Island, where environmental heterogeneity was greatest (13.2% for colony distance, and 3.1% for depth; Table 4), and least variation at Puffin Island, where environmental heterogeneity was lowest (1.6% for colony distance, and 0.4% for depth; Table 4).

The probability of habitat selection of different water depths changed during the tidal cycle following a similar pattern between Skomer Island (medium heterogeneity) and Rathlin Island (high heterogeneity), with some overlap at Puffin Island (low heterogeneity). At all colonies, during slack low water kittiwakes had a higher probability of selecting deeper water and a lower probability of selecting shallow water (Fig. 4). At Skomer Island and Rathlin Island (medium and high heterogeneity), during the flood tide kittiwakes had the highest probability of selecting shallow water and the lowest probability of selecting deep water, whereas this was the case during high water (the subsequent tidal stage) at Puffin Island (low heterogeneity) (Fig. 4).

The probability of remaining close to the colony changed during the tidal cycle (Fig. 3 and 4) depending on habitat preference by bathymetry. During low water, the
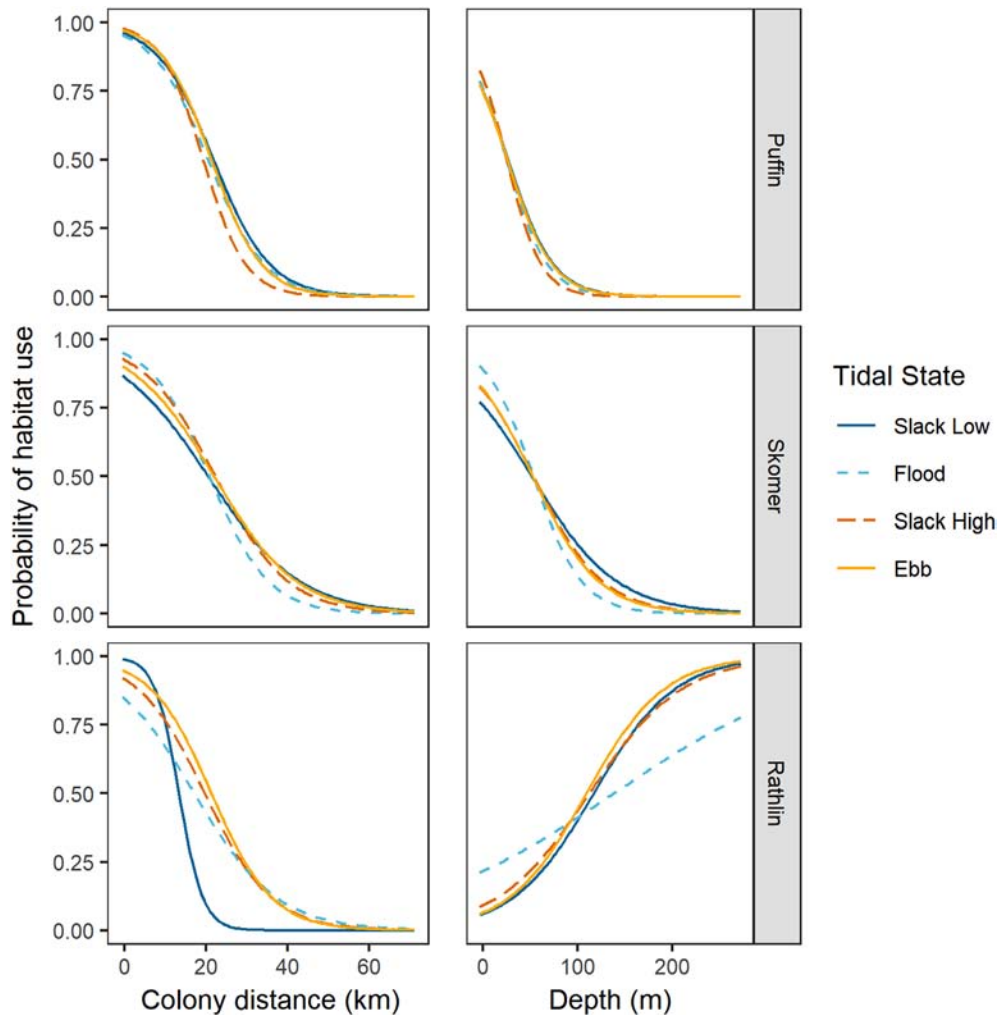
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Figure 3. Probability of habitat use whilst foraging at different distances to the colony (left) and at varying water depths (right) for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Curves from full models of all colonies together (Table 2, 3). At all colonies, kittiwakes preferentially remain close to the colony. At Puffin Island and Skomer Island, where water depth close to the colony is shallower, kittiwakes preferentially forage in shallow water, whereas at Rathlin Island, which is adjacent to very deep water, kittiwakes preferentially forage in deep water.

bathymetry model showed that individuals had the lowest probability of being in shallower waters at all colonies (Fig. 3 and 4), and accordingly kittiwakes had lower probability of remaining close to the colony where adjacent waters were shallow (Puffin Island and Skomer Island). In contrast, kittiwakes had highest probability of remaining close to the colony where adjacent waters were deep (Rathlin Island) (Fig. 4).

Table 4. Variance explained by models of each environment variable (distance to colony or depth) separately for each of the three study colonies, both with and without the two way interaction between the environment (distance to colony or depth) variable and tidal state. Models are generalised linear mixed effects models with a binomial response of habitat use (used = 1, available = 0), with Bird ID and Trip ID included as random effects. Environmental heterogeneity is low at Puffin Island, medium at Skomer Island and high at Rathlin Island.

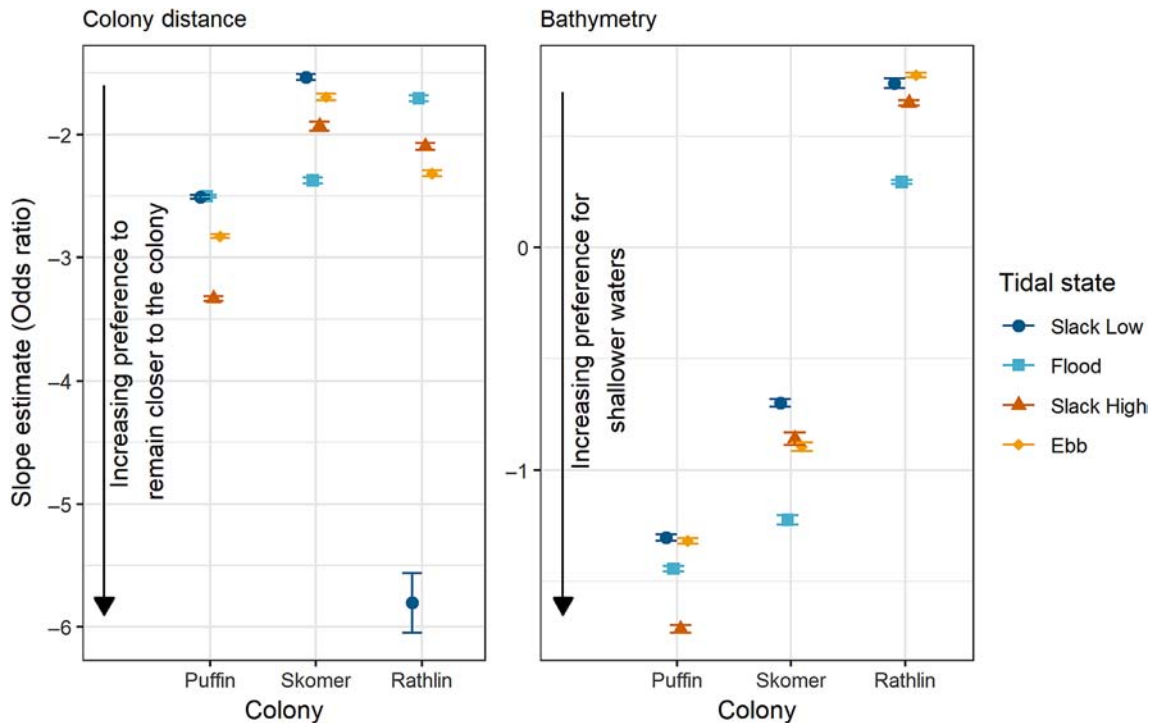| Two-way interaction	Colony	Marginal R^2 (%)		Difference in R^2 (%)
		With two-way interaction	Without two-way interaction	
Distance to colony × tide	Puffin	65.1	63.5	−1.6
	Skomer	34.6	32.8	−1.8
	Rathlin	63.0	49.9	−13.2
Depth × tide	Puffin	19.7	19.3	−0.4
	Skomer	17.5	15.7	−1.8
	Rathlin	22.2	19.0	−3.1

Figure 4. Kittiwake habitat preferences for greater distances from the colony (left) and greater water depths (right) from models of habitat selection ran separately at each colony and including the effect of tidal state (see methods text for details). All slope values for colony distance (left) are negative, which indicates a general preference for foraging closer to the colony. Lower slope values (or more negative) indicate a stronger preference for areas closer to the colony compared to other tidal states. At Puffin Island and Skomer Island, slope values for bathymetry (right) are negative, indicating an overall preference for shallower water, whereas slope values at Rathlin Island are positive, indicating an overall preference for deeper waters. Lower slope values indicate a stronger preference for shallow waters compared to other tidal states. Tidal states are defined as slack low: >5 h either side of high water; flood: 1–5 h before high water; slack high: 1 h either side of high water; and ebb: 1–5 h after high water. Environmental heterogeneity is low at Puffin Island, medium at Skomer Island and high at Rathlin Island.

Discussion

Our study demonstrates that, in addition to the previously documented effect of proximity to the colony, habitat selection by kittiwakes was influenced by depth and tidal state, and that this latter effect was greater in a more heterogeneous local environment. This means that kittiwakes showed temporal variation in spatial habitat selection over a predictable cycle that alters the foraging environment at time scales relevant to single foraging trips. Furthermore, we show that environmental heterogeneity increased temporal variability in habitat selection, suggesting that adaptations to the local environment and short-term cycles could maximise foraging efficiency, and therefore fitness gains.

Foraging theory predicts that animals should adapt to the distribution of their target resources (Stephens and Krebs 1986), and temporal changes in habitat preference have been demonstrated in response to long-term resource changes, such as seasonal cycles (Guyot et al. 2017). In this study, we provide evidence supportive of short-term changes in habitat selection that are most likely an adaptation to cyclic changes in resource availability. We found that kittiwake habitat selection of different bathymetries varied temporally during the

tidal cycle, a ubiquitous process in the coastal marine environment that can shape resource distribution because of interactions between tidal currents and the bathymetric landscape (Zamon 2003). This behavioural response is therefore most likely an adaptation to enhanced resource availability or accessibility (Ladd et al. 2005). For example, we found a lower probability of kittiwake presence in deep water during the flood tide, when elsewhere fish have been found to be more dispersed throughout a deep channel (Zamon 2003), and therefore less accessible to surface-feeding kittiwakes. We also found lower probability of kittiwake presence in shallow water during low tide, which concurs with when previous studies in the North Sea have found lowest numbers of pelagic fish in shallow waters (Couperus et al. 2016). Kittiwakes may be selecting to forage in shallower waters during flood tides because currents improve prey accessibility for surface feeders. When rearing small chicks, kittiwakes are unable to time their departure from the colony with the tide because they are constrained by their partner's behaviour, which highlights the importance of adapting their spatial behaviour to match temporal conditions. Such behavioural adaptation may be possible because of the predictability and regular repetition of the 12.4-h tidal cycle. Whilst tide-driven resource changes are

unique to the marine environment, predictable diurnal cycles that alter physical (Deser 1994, Dai 2001) and biological environments (Rydell et al. 1996, Timewell and Mac Nally 2004, Brierley 2014) are commonplace. Our results suggest that predictable cycles may therefore have significant effects on where and when foraging animals can locate resources in many ecosystems.

As well as the influence of a predictable temporal cycle on behaviour, here we find that environmental heterogeneity increases behavioural adaptation to resource changes. Kittiwakes in the more heterogeneous environments modified their spatial foraging behaviour over the tidal cycle more than those in the more homogeneous environment, showing greater variation in habitat preference between tidal stages both in respect to distance to the colony and depth. We suggest that this occurs because environmental heterogeneity drives the effect of a temporal cycle on resource changes, and therefore also causes spatial variability in temporal resource changes. In contrast, in more homogeneous environments, the features that cause tidal resource changes are reduced or absent, and therefore behaviour changes less over the tidal cycle. This location-specific mechanism could also explain why previous studies of prey fish and seabirds find varying magnitudes of responses to different stages of the tidal cycle (Irons 1998, Embling et al. 2012, Cox et al. 2013), as observations in a single site may not reveal the full extent of behaviour in relation to the surrounding physical environment. Research has shown that behavioural adaptations to environmental heterogeneity can prove profitable to individual foragers (Klaassen et al. 2006) and whole communities (Waugh and Weimerskirch 2003) by increasing prey encounter rates and enabling species coexistence through resource specialisation. Our results support these studies, and provide additional evidence that behavioural adaptation to environmental heterogeneity is likely beneficial, potentially through maximising prey location.

When travelling away from their breeding site, central place foragers experience a tradeoff between distance from the colony and habitat quality (Olsson and Bolin 2014). Individuals can be constrained to remain close to the colony unless limited resources require them to seek prey further away (Elliott et al. 2009, Burke and Montevecchi 2009), potentially at the cost of breeding success (Boersma and Rebstock 2009, Chivers et al. 2012). Here, we confirm that distance to the colony is a major driver of habitat selection; at all study sites kittiwakes had a higher probability of remaining close to the colony. The effect of distance to the colony on habitat selection was greater than that of bathymetry, likely because of energetic constraints. Nevertheless, we observed changes in the probability of remaining close to the colony over the tidal cycle, which importantly reflect bathymetry influences on kittiwakes that are consistent between study sites. Not only does this add weight to the theory that resource availability drives habitat selection changes, but it stresses the importance of apparently fine-scale environmental differences on

behaviour. The interactions between the tidal cycle and distance to the colony or depth might appear to explain relatively small amounts of model variance. However, they are comparable to the variance explained by oceanic fronts (Cox et al. 2016), which are now widely accepted to be important features enhancing prey availability to marine top predators (Scales et al. 2014, Cox et al. 2016). Furthermore, for animals with such finely balanced energy budgets (Collins et al. 2016), the fact that these behavioural changes occur repeatedly within central-place foraging suggests that the ability to adapt to predictable resource changes in otherwise variable environments could make all the difference between breeding success and failure.

Conclusions

In this study, we demonstrate that a predictable temporal cycle can influence spatial movement behaviour at time scales not previously demonstrated, and that environmental heterogeneity can enhance the magnitude of this effect. Such shifts in behaviour across multiple environments show a key adaptation of animals to maximise foraging efficiency by matching their own distribution to that of their resources at hourly resolution. We have studied this process in the marine environment, and provide new evidence in support of the tidal coupling hypothesis using direct measurements of seabird behaviour in contrasting environments, highlighting the complex nature of interactions between predators, prey, and their surrounding physical features. Kittiwakes are an environmental indicator species (Wanless et al. 2007), and thus results may have applied relevance for marine management. For example, in the context of tidal energy installations, which have the potential to significantly reduce tidal flow dynamics in surrounding areas (Pérez-Ortiz et al. 2017), the loss of predictable prey fluctuations could have negative consequences for animals that are adapted to tidal changes. Furthermore, as temporal cycles and environmental variability are ubiquitous in nature, the results of this study highlight that interactions between fine-scale resource distribution changes and the physical environment may shape predator behaviour across many ecosystems.

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