



RESEARCH ARTICLE

Environmental heterogeneity promotes individual specialisation in habitat selection in a widely distributed seabird

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Abstract

1. Individual specialisations in behaviour are predicted to arise where divergence benefits fitness. Such specialisations are more likely in heterogeneous environments where there is both greater ecological opportunity and competition-driven frequency dependent selection.
2. Such an effect could explain observed differences in rates of individual specialisation in habitat selection, as it offers individuals an opportunity to select for habitat types that maximise resource gain while minimising competition; however, this mechanism has not been tested before.
3. Here, we use habitat selection functions to quantify individual specialisations while foraging by black-legged kittiwakes *Rissa tridactyla*, a marine top predator, at 15 colonies around the United Kingdom and Ireland, along a gradient of environmental heterogeneity.
4. We find support for the hypothesis that individual specialisations in habitat selection while foraging are more prevalent in heterogeneous environments. This trend was significant across multiple dynamic habitat variables that change over short time-scales and did not arise through site fidelity, which highlights the importance of environmental processes in facilitating behavioural adaptation by predators.
5. Individual differences may drive evolutionary processes, and therefore these results suggest that there is broad scope for the degree of environmental heterogeneity to determine current and future population, species and community dynamics.

KEYWORDS

behavioural consistency, foraging behaviour, habitat selection, kittiwake, movement ecology, seabird

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1 | INTRODUCTION

Through habitat selection, individuals optimise their use of the environment to maximise fitness (Rosenzweig, 1981). Where all individuals in a population profit from the same foraging, breeding or refuge habitats, habitat selection can shape speciation (Webster et al., 2012). However, over shorter time-scales, mean population fitness may actually be compromised by identical behaviour of all individuals (Araújo et al., 2011; Bolnick et al., 2003). For example, if all individuals share the same optimal habitat, interference competition could limit fitness gains (Araújo et al., 2011; Riotte-Lambert et al., 2015). Alternatively, distinct phenotypes may require different habitats for fitness gain (Polis, 1984). In either case, phenotypic diversity in habitat selection, whereby individuals specialise on unique subsets of the habitat relative to the population, can offer a fundamental adaptation to the environment (Edelaar & Bolnick, 2019).

The degree of environmental heterogeneity characterises the range of available habitats to a given population (Sparrow, 1999). Heterogeneity in the physical environment can create opportunities to specialise on different habitat types (Araújo et al., 2011; Bolnick & Ballare, 2020), potentially at the cost of greater intraspecific competition if many individuals select patches with similar habitat characteristics (López-Bao et al., 2011; Trevail, Green, Sharples, Polton, Miller, et al., 2019). Therefore, in heterogeneous environments, we predict individual specialisations in habitat selection to persist because they enable individuals to select habitat types where the benefit of lower exploitative competition (i.e. fewer individuals competing for the same pool of resources), and therefore greater resource gain, outweighs the risk of interference competition (i.e. direct competition between individuals, such as aggression) at resource patches (Edelaar et al., 2017).

In response to heterogeneity in habitat type, individual specialisations in habitat selection have recently been demonstrated in brown bears *Ursus arctos* (Leclerc et al., 2016), but were almost absent in a study of Scopoli's shearwaters *Calonectris diomedea* (Courbin et al., 2018). Such differences in observed prevalence of

individual specialisations in habitat selection could be caused by environmental heterogeneity; however, this has not been tested before. We outline a framework (Figure 1), based on previous literature on the evolutionary ecology of individual specialisations, by which the degree of environmental heterogeneity could shape the prevalence of individual specialisations in habitat selection within populations. In more homogeneous environments, natural selection should favour a common phenotype among all individuals of population that is well matched to the available environment (Edelaar et al., 2017). In contrast, in more heterogeneous environments, natural selection ought to favour a diverse range of individual phenotypes within a population, as individuals are able to access a diversity of optimal habitats, that is, opportunity (Edelaar & Bolnick, 2019), and minimise exploitation competition.

In this study, we test the proposed framework (Figure 1) using a large dataset of individual foraging habitat selections of a widely distributed seabird species, the black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwakes'). We tracked kittiwakes from 15 populations along a natural gradient of environmental heterogeneity during the breeding season, when, as central place foragers, they are constrained by the energetic requirements of offspring and partners to forage near to breeding sites (Davoren & Montevecchi, 2003). Kittiwakes are surface feeders, and are therefore also constrained in the type of prey species that they have access to, feeding near exclusively on lesser sandeel *Ammodytes marinus*, in the North Sea and on sandeel and surface shoaling clupeids elsewhere across their UK range (Chivers et al., 2012; Frederiksen et al., 2004). Furthermore, in marine ecosystems, dynamic oceanographic conditions are important drivers of resource availability, and therefore habitat selection of predators (Wakefield et al., 2017; Weimerskirch, 2007). Indeed, kittiwakes can adjust their habitat selection, most likely to maximise resource acquisition (Trevail, Green, Sharples, Polton, Arnould, et al., 2019), and yet appear to experience greater levels of intraspecific interference competition at resource patches in more heterogeneous environments (Trevail, Green, Sharples, Polton, Miller, et al., 2019).

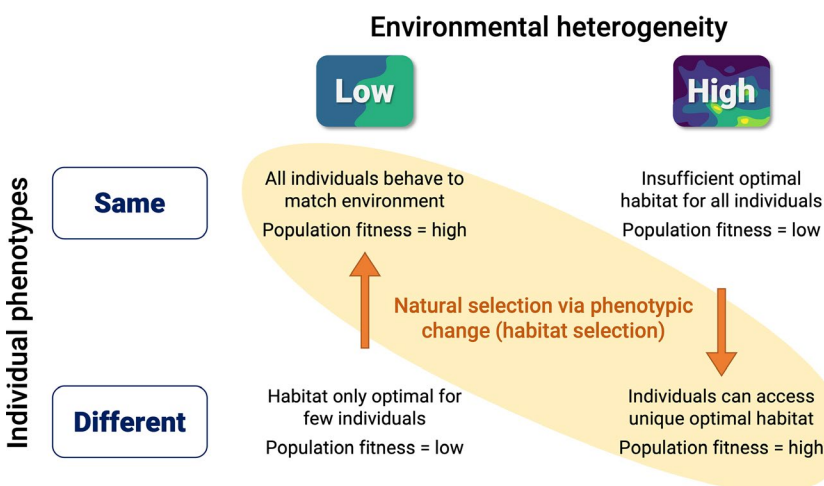


FIGURE 1 Framework by which we would expect selection (orange arrows) to favour populations of common phenotypes that share optimal habitats where heterogeneity is low, and individuals with unique habitat specialisations where heterogeneity is high

First, we establish whether, at the species, population and individual levels, kittiwakes select foraging habitat according to a set of environmental variables that can influence prey accessibility. Second, we test the proposed framework (Figure 1) to determine whether the degree of environmental heterogeneity influences the prevalence of individual specialisations in habitat selection, while foraging, between populations. Specifically, we hypothesise that for populations with more heterogeneous local environments, individual kittiwakes will be more specialised in their foraging habitat selection over a suite of environmental variables; that is, that individuals use different subsets of the available habitat with specific environmental features relative to other individuals. Finally, because environmental heterogeneity in the dynamic marine environment reflects the complexity of habitat types that shape resource fluctuations over both space and time (Trevail, Green, Sharples, Polton, Arnould, et al., 2019), we establish whether habitat selection specifically (i.e. tracking habitat types), rather than fidelity to particular foraging site locations, is the mechanism by which individual specialisations in habitat selection while foraging arise in these populations (Merkel et al., 2020). To do so, we test whether environmental heterogeneity influences a population's degree of individual fidelity to specific foraging sites.

2 | MATERIALS AND METHODS

2.1 | Kittiwake GPS tracking

To determine habitat selection of kittiwakes while foraging, we tracked breeding adults from 15 colonies around the United Kingdom and Ireland using GPS loggers (Mobile Action i-GotU GT-120) attached to the back or tail feathers that in all cases weighed <5% of individual's body mass. Full details of tracking procedures can be found in the original publications of the data (Trevail, Green, Sharples, Polton, Arnould, et al., 2019; Wakefield et al., 2017). Here, we use data from 415 individuals at 15 colonies between 2010 and 2017: Bardsey (NW Wales; 2011, n individuals = 8), Bempton Cliffs (E England; 2010–13 and 2015, n = 59), Copinsay (Orkney Islands, N Scotland; 2010–12, n = 26), Coquet (NE England; 2011–12, n = 26), Colonsay (W Scotland; 2010–14, n = 69), Filey (E England; 2013 & 2015, n = 26), Fowlshough (E Scotland; 2012, n = 13), Isle of May (E Scotland; 2013, n = 16), Lambay (E Ireland; 2010, n = 10), Muckle Skerry (Orkney Islands, N Scotland; 2012–2014, n = 26), Puffin Island (NW Wales; 2010–16, n = 63), Rathlin (Northern Ireland; 2017, n = 17), Skomer (SW Wales; 2016–17, n = 14), St Martins (Isles of Scilly; 2010–11, n = 28) and Winnyfold (E Scotland; 2012, n = 14). Full sample sizes, tracking dates and colony locations are given in Supporting Information Appendix A.

2.2 | Identification of foraging locations

We considered departures from the colony as foraging trips when locations were >500 m from the colony, and when the total time away

from the colony was >14 min to eliminate departures because of disturbance (Trevail, Green, Sharples, Polton, Arnould, et al., 2019). We used a hidden Markov model to classify behaviour into rest, forage or transit based on distributions of step lengths and turning angles using the R package *moveHMM* (Michelot et al., 2016), as previously published on this dataset (Trevail, Green, Sharples, Polton, Miller, et al., 2019; Supporting Information Appendix B). Herein, we only undertake analyses on kittiwake locations classed as foraging, that is, those characterised by short step lengths and wide turning angles.

2.3 | Environmental metrics

To understand habitat selection of kittiwakes we used six environmental metrics that influence resource distributions in coastal seas (Waggitt et al., 2018): (a) bathymetry (sea floor depth, m); (b) potential tidal stratification ($\log_{10}(m^{-2} s^3)$), (c) sea surface temperature (SST, °C), (d) ocean front strength (°C/1.2 km), (e) distance to the nearest ocean front (km) and (f) ocean front persistence (fraction of cloud-free observations of a pixel for which a front was detected), described in full in Supporting Information Appendix C. Bathymetry and potential tidal stratification, which both remain static over time, determine the vertical structure of the water column and therefore prey accessibility to surface foragers (Scott et al., 2013). SST and ocean fronts (horizontal boundaries between water masses that can aggregate nutrients and prey) indicate processes that can enhance local productivity (Benazzouz et al., 2014; Scales et al., 2014), and are dynamic variables that fluctuate over time. Resource availability and distributions in the marine environment are known to be a result of all above environmental features collectively (Waggitt et al., 2018), and therefore it is heterogeneity across all environmental variables together that defines the unique foraging environment at each colony (Trevail, Green, Sharples, Polton, Miller, et al., 2019, Supporting Information Appendix C: Figure C2).

We used values of environmental heterogeneity calculated for these study colonies in Trevail, Green, Sharples, Polton, Miller, et al. (2019). Environmental heterogeneity is a single value for each colony, per year, which indicates the spatial dissimilarity of habitats within the foraging range (Anderson et al., 2006). It is calculated using a principal coordinate analysis of seasonal composites of all six environmental variables detailed above (Trevail, Green, Sharples, Polton, Miller, et al., 2019). Standardised values of randomly selected points from within foraging ranges at each colony are placed along principal coordinate axes in unconstrained ordination space using the functions *vegdist* and *betadisper* in the R package *VEGAN* (Oksanen et al., 2018). Specifically, environmental heterogeneity is the mean Euclidean distance of points at each colony from the colony centroid along all principle coordinate axes; higher values indicate greater heterogeneity.

Correlations between heterogeneity computed over short time-scales (weekly and annually) and the colony-mean value were high (Trevail, Green, Sharples, Polton, Miller, et al., 2019), suggesting that colony-specific environmental heterogeneity remains relatively

constant over time. Furthermore, we found no link between environmental heterogeneity and the size of colony foraging radii (Trevail, Green, Sharples, Polton, Miller, et al., 2019). In heterogeneous environments, therefore, although the size and location of resource patches may change over short time-scales, the structure of the physical environment is overall more likely to cluster resources into patches (Trevail, Green, Sharples, Polton, Miller, et al., 2019). Thus, our measure of heterogeneity is primarily a property of the colony's location and surrounding environment, rather than a function of temporal factors. As such, herein we use a single value of environmental heterogeneity for each colony (as in Trevail, Green, Sharples, Polton, Miller, et al., 2019) to understand how individual specialisations arise and persist between colonies. In support of this, analyses of individual specialisation in habitat selection while foraging using the annual value of environmental heterogeneity yield the same results as those presented below (Supporting Information Appendix C: Figure C3), most likely because variability in environmental heterogeneity within colonies is less than the variability between colonies.

2.4 | Kittiwake habitat selection

Resource selection models are commonly used to understand animal habitat selection (Manly et al., 2002), and recently to account for individual-specific variation (Courbin et al., 2018; Leclerc et al., 2016; Muff et al., 2020). Here, we use methods described in Muff et al. (2020) to quantify individual specialisations in habitat selection for multiple populations. Habitat selection (binomial response; available = 0 or used = 1) was modelled in response to each environment variable in turn in order to extract individual habitat selection slopes (Courbin et al., 2018). In support, correlations between environmental variables were generally low (Supporting Information Appendix C: Figure C4) and all environmental variables were retained by AIC selection in a full model (excluding random slopes because of complexity). To account for central place foraging behaviour, we included distance to the colony as a fixed effect (Trevail, Green, Sharples, Polton, Arnould, et al., 2019). Colony distance, bathymetry, front strength, front persistence, and front distance were square-root transformed to approach a Gaussian distribution, and all variables were standardised (0-centred mean and standard deviation of 1) prior to analyses to facilitate comparisons between models (Supporting Information Appendix C: Figure C5).

As a measure of the available habitat, we selected two random points for each used point from within the maximum foraging range of kittiwakes specific to each colony and year (Supporting Information Appendix D). We use a constant ratio of used to available points, so that variability in model intercepts truly reflects individual differences in habitat selection, rather than a user-defined sample design (Fieberg et al., 2010; Muff et al., 2020). To avoid selection bias where remote sensing data (SST and ocean fronts) were obscured by, for example, cloud cover, and against coastal regions outside of gridded modelled tide data (stratification), we only retained used locations where environment data were available for the

used point and both available data points. This meant that different numbers of foraging locations were retained for each environment variable (Supporting Information Appendix D); at a minimum, models included 75,311 used points from 1,270 trips and 378 individuals (max = 137,774 used points, 1,534 trips and 410 individuals).

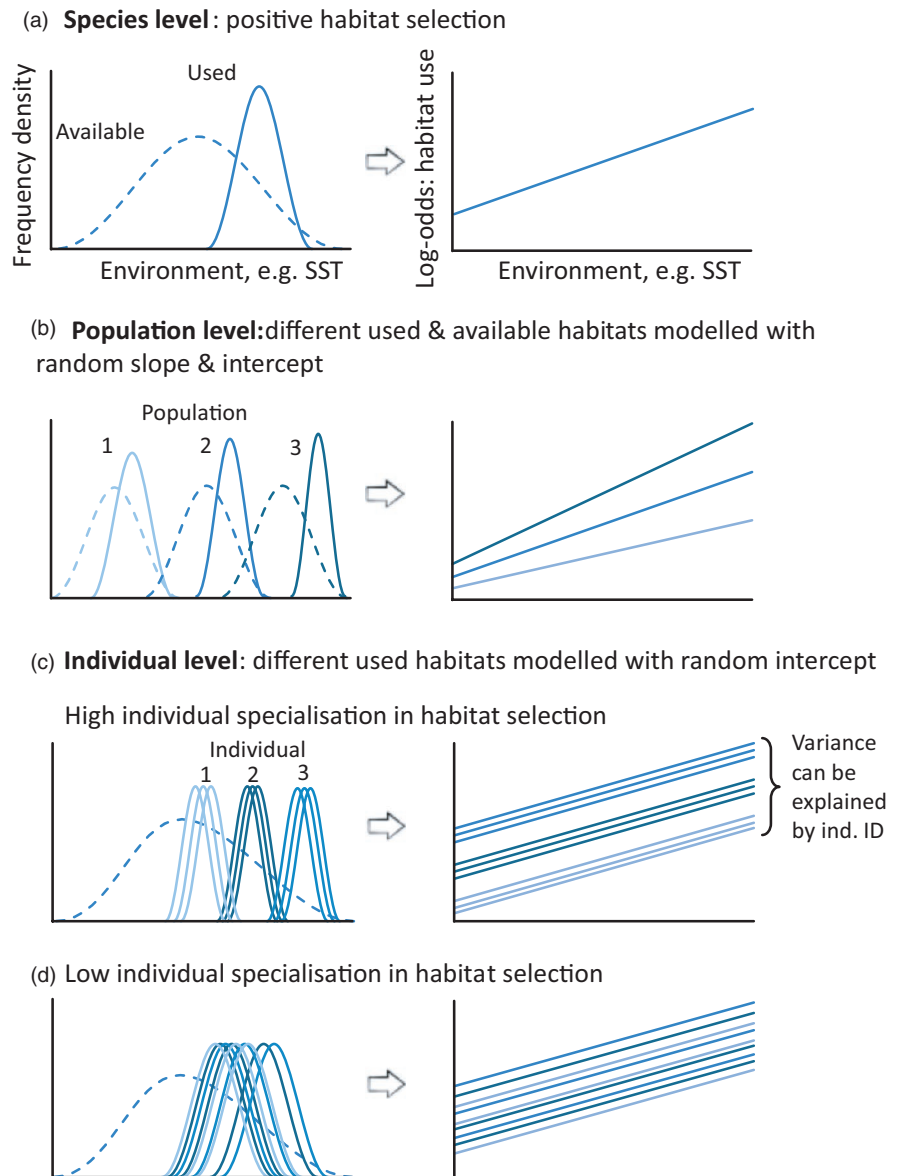
Models were implemented using a binomial error structure with a logit link using the *glmer* function of the R package *LME4* (Bates et al., 2015). We included a random intercept and slope for colony year to account for different habitat availability; and a random intercept for each foraging trip ID, unique to the individual and population, to account for individual habitat selection (Figure 2). We selected the most suitable fixed effects structure based on Akaike information criterion (AIC) values in backward stepwise selection, in all cases retaining both the environmental variable in question and colony distance in the model (Supporting Information Appendix E: Tables E1 and E2). We ensured model fit by calculating the area under the receiver operator characteristic curve (AUC; Zweig & Campbell, 1993) predictive power, sensitivity and specificity (Trevail, Green, Sharples, Polton, Arnould, et al., 2019); Supporting Information Appendix E5: Table E3.

To interpret habitat selection at the species level, we took the global intercept and slope from models of each environmental variable (Figure 2a). Negative slope values indicate preference for lower than average values compared to the available environment, and conversely, positive slope values indicate preference for higher than average available values. To understand how populations varied in habitat selection, we extracted slope coefficients from the habitat selection models for each colony year (Figure 2b). As a measure of individual habitat use, we extracted parameter estimates for each trip as random intercepts (Figure 2c). Parameter estimates are presented on the log-odds scale, and for colony distance, bathymetry, front strength, front persistence, and front distance are presented as square-root transformed.

2.5 | Quantifying individual habitat specialisations

To test whether environmental heterogeneity influenced the prevalence of individual habitat specialisations, we first calculated the degree of individual specialisations in habitat selection as the adjusted repeatability index of trip intercepts (Courbin et al., 2018), using the R package *RPT*R (Nakagawa & Schielzeth, 2013) for each variable, and for each year and colony to reflect the hierarchical nature of the data (observations, trips, individuals, years and colonies). Repeatability is the proportion of total model variance explained by within-individual differences, and ranges from 0 to 1; where high values (approaching 1) indicate high prevalence of individual habitat specialisations within the local population, whereby individual ID explains a large amount of model variance (Figure 2). Conversely, low values of repeatability (approaching 0) indicate low prevalence of individual specialisations in habitat selection within the local population, whereby individual ID explains a small amount of model variance. Because the repeatability of random slope coefficients from habitat selection models has not previously been used to derive individual specialisation in habitat

FIGURE 2 Schematic to show how resource selection functions using random slopes and intercepts modelled habitat selection at (a) the species; (b) population; and (c) individual level. Frequency density plots show available habitat in dashed lines and used habitat in solid lines. Individual specialisation in habitat selection was quantified for each population using repeatability analyses to calculate model variance explained by individual



selection across multiple populations, we validated the use of *rptR* for this purpose on simulated data (Supporting Information Appendix F).

We then compared the value of repeatability of habitat selection calculated for each colony and year to the colony-mean value of environmental heterogeneity (described above, as in Trevail, Green, Sharples, Polton, Miller, et al., 2019) using linear regression for habitat selection of each environmental variable in turn. We accounted for temporal variability, however, found no effect of year as a random effect in mixed effects models and thus present results from linear regressions only. To verify that differences in individual specialisation in habitat selection were not an artefact of the duration of tracking time or the inclusion of individuals with few trips, we confirmed that the mean value of repeatability for habitat selection was not linked to the mean number of foraging trips recorded per individual across colonies; linear regressions for each environmental variable were not significant ($p > 0.05$).

Population size can be an indicator of conspecific density and therefore intraspecific competition (Lewis et al., 2001), a key driver

of individual specialisation. To test whether population density was linked to individual specialisation in habitat selection among these populations, we used linear regression to compare colony-year values of repeatability with colony sizes (Supporting Information Table A1) from Seabird 2000, the most relevant complete seabird census of the United Kingdom and Ireland (Mitchell et al., 2004), which offers a valuable indicator of relative population sizes for the purpose of this study (Trevail, Green, Sharples, Polton, Miller, et al., 2019).

2.6 | Quantifying site fidelity

An apparent effect of environmental heterogeneity on individual habitat selection specialisation could arise if individuals were faithful to specific foraging sites in all environments, and/or more site faithful in more heterogeneous environments. To assess whether site fidelity or habitat selection is the mechanism by which specialisation arises,

we quantified individual site fidelity using a nearest neighbour similarity index following methods in Patrick and Weimerskirch (2017) and Harris et al. (2020). We first aggregated consecutive foraging locations into foraging sites, represented by a single pair of central coordinates. For each foraging site in turn as the focal site, we randomly paired the focal site with a foraging site from the same individual from a different trip (within-individual comparison), and a foraging site from a different individual (between-individual comparison). Focal sites were taken from individuals with more than one trip in any given year, and comparison sites were drawn from all individuals within the same colony and year. The similarity index was calculated as the proportion of between-individual paired sites that were closer to the focal site than the within-individual paired site. The index is bounded between 0 and 1, and for interpretability we inverted it ($1 - x$) so that values approaching 1 indicate high individual site fidelity, whereas values approaching 0 indicate low individual site fidelity (Harris et al., 2020). We then used a binomial generalised linear regression with individual ID as a fixed effect to derive a single estimate of site fidelity for each individual from the similarity indices of all focal foraging sites, accounting for time difference (days) between paired sites as a fixed effect. We ran 1,000 iterations of the randomisation process, and then calculated the mean of all 1,000 estimates per individual, giving a single value of site fidelity per individual, per year.

To understand site fidelity within these kittiwake populations, we present the median and range of site fidelity values per colony (Harris et al., 2020; Patrick & Weimerskirch, 2017). To understand whether environmental heterogeneity was linked to site fidelity, we tested for a link between colony environmental heterogeneity and the annual mean of site fidelity (distribution of estimates was Gaussian) using a linear regression (Harris et al., 2020; Trevail, Green, Sharples, Polton, Arnould, et al., 2019). Again, to verify that differences in site fidelity were not an artefact of the duration of tracking time or the inclusion of individuals with few trips, we confirmed that the mean value of site fidelity was not linked to the mean number of foraging trips recorded per individual across colonies (linear regression; $p > 0.05$).

3 | RESULTS

3.1 | Kittiwake foraging metrics

Tracking data yielded a total of 1,567 foraging trips, on average 3.78 ± 0.13 trips per individual (mean across colonies \pm SE; ranging from 1 to 19, Supporting Information Appendix A: Table A1). Trips were on average 6.5 ± 0.3 hr duration, 76.9 ± 3.0 km long, and reached a maximum of 23.3 ± 0.8 km from the colony (Supporting Information Appendix A: Table A2).

3.2 | Kittiwake habitat selection

At the species level, as expected, kittiwakes preferentially foraged closer to the colony (in all models slope coefficients for

colony distance were below zero, Supporting Information Appendix G: Table G1). Results also showed that kittiwake habitat selection varied according to all environmental variables (Figure 3). On average, kittiwakes preferentially foraged in areas of shallower water (parameter estimate \pm SE = -0.23 ± 0.14), areas where the water column was likely to be more mixed, that is, weaker stratification (-0.63 ± 0.26), areas of cooler water (-0.51 ± 0.27), areas of weaker fronts (-0.32 ± 0.09), areas that were further away from fronts (0.19 ± 0.13) and lower front persistence (-0.22 ± 0.0 ; Figure 3). There was variation in habitat selection preferences of kittiwakes between colonies (Supporting Information Appendix G: Table G1 and Figure G1; shown spatially in Figure G2) and between individuals (Supporting Information Appendix G: Figure G3).

3.3 | Individual habitat specialisations

At the individual level, results show that habitat selection was repeatable with respect to all environmental variables, that is, species-level repeatability mean and standard errors were above zero (Table 1). Mean repeatability at the species level varied between 0.13 ± 0.03 (bathymetry) and 0.21 ± 0.05 (SST), and at the population varied between 0.00 (all variables) and 0.67 (potential tidal stratification, Table 1). Individual specialisations in habitat selection were more prevalent in colonies with more heterogeneous environments for all ocean front variables (Figures 4 and 5): front strength (parameter estimate \pm SE = 0.10 ± 0.03 , test statistic from linear regression: $F_{1,33} = 10.01$, $p = 0.003$); front distance (0.10 ± 0.05 , $F_{1,33} = 5.20$, $p = 0.029$); and front persistence (0.11 ± 0.03 , $F_{1,33} = 10.32$, $p = 0.003$). Individual specialisations in habitat selection were slightly higher in heterogeneous environments for bathymetry, stratification and SST; however, the differences were not statistically significant (Table 1). Model coefficients at the trip level (Supporting Information Appendix G: Figure G3) show no visible trend in total niche width with environmental heterogeneity (based on the variance between individual intercepts), indicating that repeatability is increasing because of reduced within-individual difference.

We found no link between individual repeatability in habitat selection of any environmental variable and colony size (linear regressions; in all cases $p > 0.05$). This suggests that individual specialisation in habitat selection arises in response to environmental heterogeneity, that is, the spatial structure of the physical environment and resources, rather than greater overall conspecific density, within these populations.

3.4 | Individual site fidelity

Across all study colonies, site fidelity was highly variable between individuals and colonies (Supporting Information Appendix H: Figure H1), and moderate on average (range: 0.04–0.97, median: 0.54). There was no effect of environmental heterogeneity on site

FIGURE 3 Probability of habitat selection by kittiwakes while foraging given the: bathymetry (m), potential tidal stratification ($\log_{10}(\text{m}^{-2} \text{s}^3)$), SST ($^{\circ}\text{C}$), front strength ($^{\circ}\text{C}/1.2 \text{ km}$), front distance (km) and front persistence (fraction of cloud-free observations of a pixel for which a front was detected). Selection curves are shown at the species level (solid black lines \pm SE; dashed lines) and from each colony (grey lines; parameter estimates in Supporting Information Appendix G: Table G1). Considering the propensity to remain close to the colony, kittiwakes preferentially foraged in areas characterised by shallower depths, weaker stratification, cooler temperatures, and weaker, more distant, and less persistent fronts

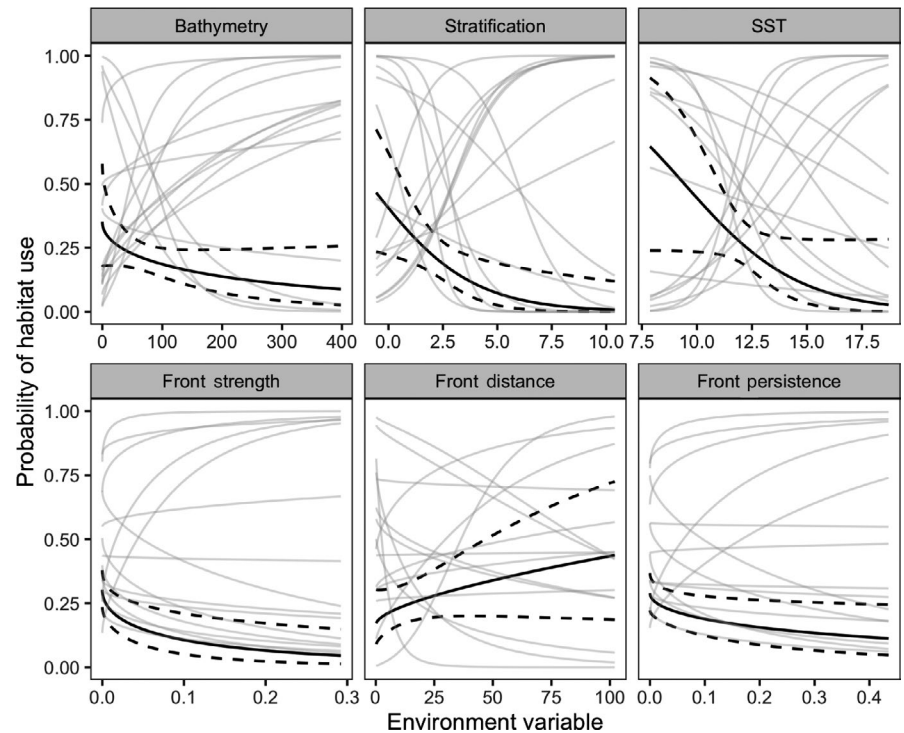


TABLE 1 Individual habitat specialisations of kittiwakes while foraging, here showing the mean and range of repeatability values among all populations, and the effect of environmental heterogeneity on repeatability, where parameter estimates and test statistics are from linear regressions. Repeatability varies from 0 (absent) to 1 (unique behaviour of all individuals)

Variable	Individual repeatability in habitat selection		Effect of environmental heterogeneity			
	Mean (\pm SE)	Range between colonies	Relationship	Parameter estimate (\pm SE)	Test statistic	<i>p</i> -value
Bathymetry	0.13 \pm 0.03	0.00–0.43	Marginal increase	0.06 \pm 0.03	$F_{1,33} = 4.09$	0.051
Potential tidal stratification	0.18 \pm 0.04	0.00–0.62	Marginal increase	0.05 \pm 0.03	$F_{1,33} = 2.71$	0.109
SST	0.21 \pm 0.05	0.00–0.52	Marginal increase	0.07 \pm 0.04	$F_{1,33} = 3.01$	0.092
Front strength	0.18 \pm 0.04	0.00–0.47	Increase	0.10 \pm 0.03	$F_{1,33} = 10.01$	0.003
Front distance	0.19 \pm 0.05	0.00–0.54	Increase	0.10 \pm 0.05	$F_{1,33} = 5.20$	0.029
Front persistence	0.18 \pm 0.04	0.00–0.52	Increase	0.11 \pm 0.03	$F_{1,33} = 10.32$	0.003

Values in bold indicate a significant relationship ($p < 0.05$).

fidelity ($F_{1,33} = 0.001$, $p = 0.96$), confirming that habitat selection is the mechanism of individual specialisation here.

4 | DISCUSSION

As predicted by our conceptual framework, we demonstrate that kittiwakes showed greater individual specialisation in habitat selection in more heterogeneous environments. This pattern was evident across multiple environmental variables, which we also show influence kittiwake habitat selection at the species and population levels, most likely because of their effects on resource distribution and availability. These results are among early evidence of individual specialisations in habitat selection specifically (see also Bonnet-Lebrun et al., 2018; Leclerc et al., 2016), and provide evidence that

environmental heterogeneity, a known driver of resource distributions and intraspecific competition (Trevail, Green, Sharples, Polton, Miller, et al., 2019), gives rise to individual specialisations in foraging behaviour.

Individual differences are an important component of biodiversity (Dall et al., 2012). They arise both where ecological opportunity facilitates and competition favours phenotypic divergence (Bolnick et al., 2003). Environmental heterogeneity presents such a scenario (Bolnick & Ballare, 2020; Trevail, Green, Sharples, Polton, Miller, et al., 2019). In line with this prediction, we found that individual specialisations in habitat selection are more likely to occur in heterogeneous environments, thus adding to a growing body of literature demonstrating that resource heterogeneity can favour individual specialisations across a suite of behaviours (e.g. Bolnick & Ballare, 2020; Edelaar et al., 2017). Furthermore, we demonstrate

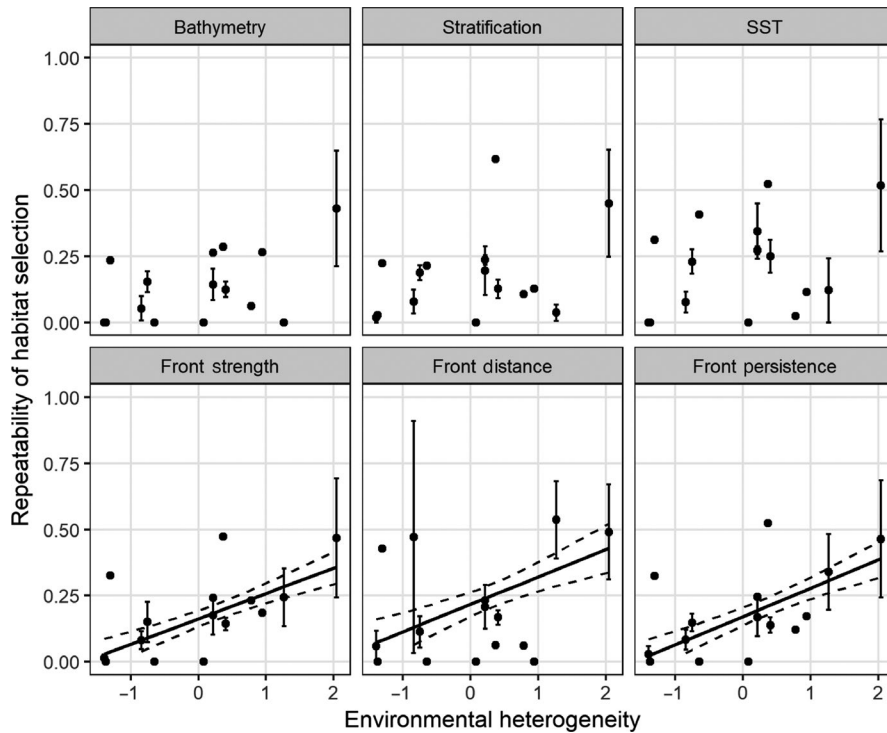


FIGURE 4 Individual repeatability of kittiwake habitat selection of different environmental variables while foraging, between populations of differing environmental heterogeneity. Each point represents a colony, and error bars show standard error between years. Significant relationships between individual repeatability and environmental heterogeneity (Table 1) are shown as linear regressions (solid lines) and standard error (dashed lines). Higher repeatability values indicate higher mean prevalence of individual habitat specialisations. Individual habitat specialisations were more prevalent in colonies with more heterogeneous environments for front strength, front distance and front persistence

that where specialisation is occurring in these populations, individuals are able to track specific habitat types rather than returning to specific locations. Individual specialisations in habitat selection may therefore offer a key mechanism in dynamic environments to reduce the detrimental effects of exploitative intraspecific competition (Svanbäck & Bolnick, 2007; Trevail, Green, Sharples, Polton, Miller, et al., 2019).

Individual specialisations in diet and foraging strategies have been extensively documented (Araújo et al., 2011; Bell et al., 2009). When quantified numerically, specialisation ranges from 0 (behaviour identical between all individuals in a population) to 1 (behaviour unique to each individual in the population). The average reported repeatability of behaviour is 0.37 (Bell et al., 2009), which is within the range of values that we find for some kittiwake populations (0.00–0.62, Table 1), although is higher than the species averages for each environmental variable (0.13–0.21, Table 1) and the repeatability values observed for many populations (Figure 4). This difference suggests that while repeatability in habitat selection by kittiwakes is high for some populations, at the species level it is most often low, in contrast to widespread reports of individual specialisations in the animal kingdom, including seabirds (Ceia & Ramos, 2015). Furthermore, our estimates of site fidelity were similar to kittiwake populations elsewhere (Harris et al., 2020), and yet are lower than comparable estimates from a more long-lived species, the black-browed albatross (Patrick & Weimerskirch, 2017). Again, this suggests that individual behavioural specialisations are often relatively low for kittiwakes, perhaps because of their faster life history compared to other taxa (Bradshaw et al., 2004) or because, ultimately, they are relatively constrained in their foraging style and prey type (Frederiksen et al., 2004). Intrinsic drivers of

behaviour may underpin some of the unexplained variation in specialisation among the study populations here, such as individual personality (Harris et al., 2020), sex specific differences (Patrick & Weimerskirch, 2014) and ontogenetic shifts in behaviours and requirements (Grecian et al., 2018; Polis, 1984). In combination, this suggests that there would be merit in further research into the incidence of animal behavioural specialisations, taking into consideration both intrinsic factors and the differences in the proximal environment.

Local adaptations are a key process in ecology and evolution, by which particular traits are favoured in the local environment regardless of their consequences for fitness elsewhere (Kawecki & Ebert, 2004). Local adaptations are ultimately maintained by natural selection; however, gene flow and temporal variability in the environment can both be limiting factors. Here, despite some potential gene flow between populations (McCoy et al., 2005) and a highly dynamic marine environment (Carroll et al., 2015), we find population variability in the strength and direction of habitat selection (Supporting Information Appendix G: Table G1 and Figures G1 and G2), as well as a link between local environmental heterogeneity and individual specialisation, which persists over time. These results demonstrate the need to consider species, population and individual adaptations when evaluating habitat preferences (Lesmerises & St-Laurent, 2017). We previously found no link between environmental heterogeneity and maximum foraging distance, indicative of overall resource abundance (Lewis et al., 2001). In combination with results presented here, therefore, this emphasises the value of local environmental heterogeneity as a constant measure of resource distributions in determining local behavioural strategies that persist over time.

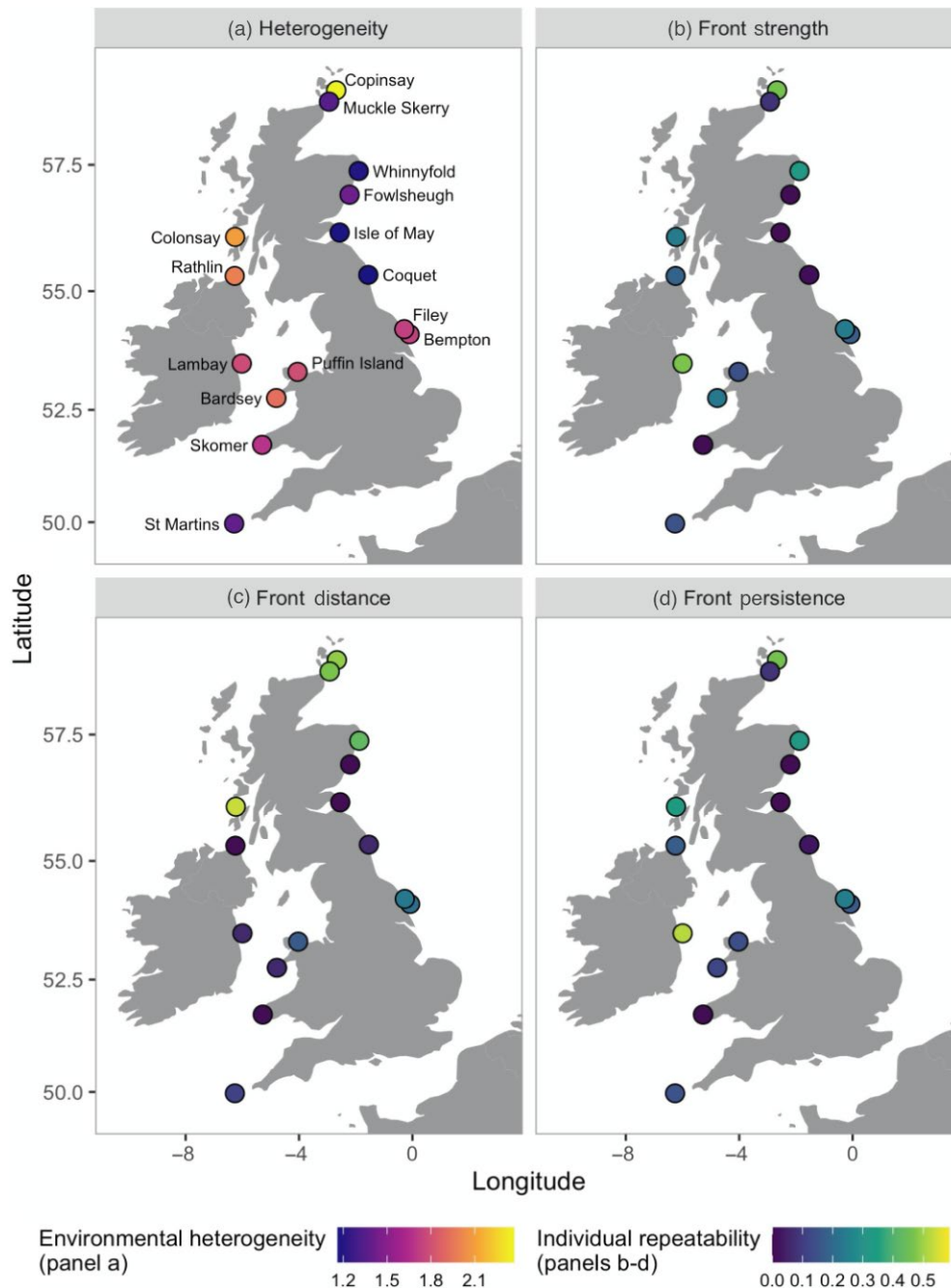


FIGURE 5 Kittiwake colonies coloured by (a) environmental heterogeneity (Trevail, Green, Sharples, Polton, Miller, et al., 2019) and (b–d) individual repeatability in habitat selection of front strength, front distance and front persistence. There was a significant correlation between environmental heterogeneity and individual repeatability in habitat selection of each three ocean front metrics, presented in Figure 4 and shown spatially here. Higher repeatability values indicate higher mean prevalence of individual habitat specialisations

In dynamic systems, ephemeral features can be key drivers of prey distributions (Sparrow, 1999; Weimerskirch, 2007). Such features are often a result of a matrix of habitat variables (Waggitt et al., 2018). Indeed, we found that kittiwake habitat selection was influenced by six oceanographic variables that influence prey distribution. On average, kittiwakes preferentially foraged in shallower, well mixed waters where tidal currents can create hotspots of shoaling fish that are the staple of kittiwakes' diet

(Zamon, 2003); and avoided deep waters where vertical mixing restricts access to prey at the surface (Carroll et al., 2015) and seasonal depletion in stratified waters reduces foraging opportunities (Behrenfeld & Boss, 2014) and sandeel availability (Jensen et al., 2003). Kittiwakes strongly selected for cooler SST, indicative of local upwelling and productivity (Benazzouz et al., 2014) and typically beneficial to many marine species at seasonal time-scales because cold-adapted plankton species are larger and

more nutritious, which positively effects the entire food web (Beaugrand et al., 2002; Carroll et al., 2015). Kittiwakes avoided warmer SSTs, hypothesised to increase metabolic cost of sandeel, inhibiting growth and reducing the time adults spend in the water column outside of burrows (Greenstreet et al., 2006). Lastly, kittiwakes selected areas of weaker, more distant, and less persistent fronts. Seasonally persistent fronts are important features for large marine taxa (Cox et al., 2016; Scales et al., 2014). This result could suggest that fronts are less important to foraging kittiwakes compared to other environmental features, or that kittiwakes are outcompeted at fronts by larger marine predators such as mammals and diving seabirds (Scales et al., 2014). However, individuals in heterogeneous environments repeatedly selected foraging areas with distinct levels of ocean fronts. This may suggest that kittiwakes are able to exploit ephemeral fronts (Cox et al., 2016), which, because of their transient nature, may still offer enhanced prey but with less interspecific competition. This result builds on previous findings that dynamic habitat characteristics can offer a key advantage to foragers (Beerens et al., 2011); specifically that fine-scale tracking and/or detection of mobile prey patches (e.g. Bastos et al., 2020; Trevail, Green, Sharples, Polton, Arnould, et al., 2019) may be particularly important to individuals where resources are more heterogeneous.

In previous studies of these populations, we found that environmental heterogeneity can create dynamic foraging opportunities for kittiwakes (Trevail, Green, Sharples, Polton, Arnould, et al., 2019). However, individuals appeared to experience greater levels of competition at resource patches in more heterogeneous environments (Trevail, Green, Sharples, Polton, Miller, et al., 2019), the results of which are detrimental to foraging success (Ainley et al., 2003; Trevail, Green, Sharples, Polton, Miller, et al., 2019). The prevalence of individual specialisations in habitat selection in heterogeneous environments, particularly in dynamic ocean front metrics, suggests a mechanism to reduce exploitative competition at fine temporal scales because not all individuals are reliant on the same type of resource patches, despite incurring a costly risk of interference competition at dynamic patches. Therefore, while individual specialisations may arise where there is ecological opportunity, perhaps they are insufficient among these populations to offset the detrimental effects of exploitative competition in the current climate, as rapid warming events and over-exploitation drive ecosystem regime shifts that are causing catastrophic declines in kittiwake populations world-wide (Carroll et al., 2015, 2017; Descamps et al., 2017; Frederiksen et al., 2004).

5 | CONCLUSIONS

Our study demonstrates the importance of environmental heterogeneity in shaping individual specialisations in habitat selection. In homogeneous environments, all individuals behave

similarly, presumably to match the environment. In contrast, in heterogeneous environments, intraspecific competition and ecological opportunity facilitate divergent habitat specialisations between individuals (Figure 1). There was no difference in site fidelity, suggesting that specialisation on habitat types rather than spatial area was the primary mechanism of adaptation to heterogeneous environments. The behavioural systems that enable individuals to adjust their phenotype to select optimal habitats have presumably evolved through the past action of natural selection (Edelaar & Bolnick, 2019). Our results therefore suggest that environmental heterogeneity could be an important driver of the degree of variation in individual phenotypes within populations, and, potentially, the scope of populations to respond to environmental change (Phillips et al., 2017). Inter-individual variation is the basis of evolution, and therefore specialisations in habitat selection in response to environmental heterogeneity are likely to be of major importance for processes such as speciation over evolutionary time-scales (Sih et al., 2004).

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CONFLICT OF INTEREST

All authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.M.T., S.C.P. and J.A.G. conceived the ideas and designed methodology; all authors contributed data; A.M.T. and S.M.H. analysed the data; A.M.T., S.C.P. and J.A.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and code are available via figshare <https://figshare.com/s/b8ef07059fe02fb8ccaf> (Trevail et al., 2021). Original tracking data are available via the Seabird Tracking Database: <http://www.seabirdtracking.org>

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article at the publisher's website.

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