



Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator

Samantha C. Patrick, Stuart Bearhop, David Grémillet, Amélie Lescroël, W. James Grecian, Thomas W. Bodey, Keith C. Hamer, Ewan Wakefield, Mélanie Le Nuz and Stephen C. Votier

S. C. Patrick (*spatrick@glos.ac.uk*), Biosciences QU116, Francis Close Hall Campus, Univ. of Gloucestershire, Cheltenham, GL50 4AZ, UK. – SPC, W. J. Grecian and S. C. Votier, Marine Biology and Ecology Research Centre, Univ. of Plymouth, Plymouth, PL4 8AA, UK. SCP also at: CEBC – CNRS, FR-79360 Villiers en Bois, France. – SCV, S. Bearhop and T. W. Bodey, Univ. of Exeter, Cornwall Campus, Penryn, TR10 9EZ, UK. – D. Grémillet and A. Lescroël, CEFÉ-CNRS, UMR5175, Montpellier, France. DG also at: Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, South Africa. AL also at: URU 420 Biodiversité et Gestion des territoires, Univ. de Rennes 1, FR-35042 Rennes Cedex, France. – K. C. Hamer and E. Wakefield, Univ. of Leeds, LS2 9JT, UK. – M. Le Nuz, LPO, Réserve Naturelle des Sept-Iles Station, FR-22560 Pleumeur Bodou, France.

Consistent intra-population variability in foraging behaviour is found among a wide range of taxa. Such foraging specialisations are common among marine vertebrates, yet it is not clear how individuals repeatedly locate prey or foraging sites at ocean-wide scales. Using GPS and time-depth loggers we studied the fine-scale foraging behaviour of central-place northern gannets *Morus bassanus* at two large colonies. First, we estimated the degree of consistency in individual foraging routes and sites across repeated trips. Second, we tested for individual differences in searching behaviour in response to environmental covariates using reaction norms, estimated from mixed effect models. Adult gannets tracked over multiple foraging trips showed repeatable between-individual differences in terminal points and departure angles of foraging trips, but low repeatability in trip duration and trip length. Importantly, individual birds showed highly repeatable dive locations, with consistently different environmental conditions (such as copepod abundance), suggesting a high degree of foraging site specialisation. Gannets also showed between-individual differences in searching behaviour along environmental gradients, such that individuals intensified searching under different conditions. Together these results suggest that widespread individual foraging consistency may represent specialisation and be linked with individual responses to environmental conditions. Such divergent searching behaviour could provide a mechanism by which consistent foraging behaviour arises and is maintained among animals that forage across large spatial scales.

There is increasing work detailing the extent of intra-population variation and individual specialisation in traits, including diet and foraging (Araujo et al. 2007, Bolnick et al. 2003). While such foraging specialisations are often determined by ontogenetic or sex differences (Shine 1989, 1991, van de Pol et al. 2009), individual-level specialisations independent of these factors are also common. Consistent individual differences in foraging site and diet are prevalent among marine vertebrates (Supplementary material Appendix A1 Table A1), which live in an environment where oceanic fronts, upwellings and other sub-surface features often lead to temporally and spatially predictable prey patches (Weimerskirch et al. 2007). Moreover, as these species breed in dense aggregations, intra-specific competition is high, which may lead to strong frequency dependent selection for divergent foraging strategies (Araujo et al. 2007).

When air-breathing marine vertebrates are constrained to forage from a central place, they may repeatedly cover huge distances between breeding sites and foraging grounds. However, how consistent individual behaviours arise and are maintained is not known. There is evidence that these

animals alter searching intensity in response to biotic and abiotic cues (Hamer et al. 2009), indicating that they use such environmental proxies to locate prey (Pinaud and Weimerskirch 2005, Votier et al. 2010). Furthermore, subsections of the population differ in the scale of their search response to environmental conditions, such as sea surface temperature and chlorophyll concentration (Pinaud and Weimerskirch 2005), demonstrating a degree of individual divergence in searching behaviour. However, the possibility that individuals increase searching under different environmental conditions has not been tested. The spatial consistency previously reported could arise from individuals searching in different locations for the same environmental conditions or for different environmental conditions at different locations. To test these hypotheses requires high-resolution data on animal movement and accurate measures of the environmental conditions over which they forage.

Bio-logging technology has been deployed extensively on marine vertebrates, resulting in some of the best data sets on fine scale foraging movements (Wilson et al. 2002). From these, it is possible to pin-point not only foraging locations,

but also changes in searching behaviour which precede these events. In this study, we used a combination of GPS and time-depth loggers, in tandem with data on marine environmental conditions, to investigate fine-scale foraging behaviour in a medium-ranging central place predator, the northern gannet *Morus bassanus* (hereafter gannet), at two large colonies in different water masses. We used repeatability measures to examine consistency in foraging routes, site fidelity and dive characteristics, and also investigate the environmental conditions under which gannets dive. These consistently divergent behaviours could themselves be termed foraging specialisations, as they demonstrate that individual niche width is considerably narrower than the population niche (previously described for trophic niche by Bolnick et al. 2003). However, as other definitions of specialisation involve a restriction in individual behaviour (Bolnick et al. 2003) which we did not test in this paper, we report consistency and divergence in our data and discuss the potential implications for specialisation. We used reaction norms, estimated from mixed effect models (Nussey et al. 2005, Dingemanse et al. 2010) to measure the change in individual search behaviour along three environmental gradients, indicative of biotic and abiotic proxies for resource availability in the marine environment. While these models, commonly applied in evolutionary biology, have been advocated to help understand both seabird responses to environmental conditions (Gremillet and Charmantier 2010) and changes in behaviour at the individual level (Dingemanse et al. 2010), they have yet to be used to study changes in individual foraging behaviour in a wide-ranging marine predator.

Material and methods

Data collection

Fieldwork was conducted on Grassholm Island, Wales, UK (51°43'N, 05°28'W) and Ile Rouzic, Brittany, France (48°54'N, 3°26'W). Data from multiple foraging trips were collected during chick-rearing from 1–10 June 2010 (Rouzic) and 3–21 July 2010 (Grassholm), for pairs with chicks aged 4–6 weeks. Birds on Rouzic bred approximately one month earlier than those on Grassholm (Wanless et al. 2008, Le Nuz unpubl.). On Grassholm about 40 000 pairs of gannets breed annually and here 26 individuals were fitted with GPS loggers (mass 30 g), and programmed to record locations every two min. All the loggers were recovered and 18 had useable data. In addition, time-depth recorders (6 g) were deployed on ten of these birds, recording depth every 0.1 s when submerged. GPS devices were attached at the base of the tail and TDRs under the central two tail feathers using TESA tape and previous work suggests that loggers such as these have no adverse effects on breeding gannets (Garthe et al. 2007, Hamer et al. 2007, 2009). On Rouzic about 20 000 pairs of gannets breed and here 19 individuals were fitted with GPS loggers (mass 60 g), attached using TESA tape and programmed to collect location fixes every 1 s. These data were then re-sampled to a resolution of 2 min to allow direct comparisons between colonies and of the 16 recovered, 13 of these loggers had useable data. No dive data were collected from Rouzic.

Measuring environmental gradients

Spring 2010 sea-surface temperature (SST, °C; <<http://modis.gsfc.nasa.gov/>>), spring 2010 chlorophyll-a concentration (chl-a, mg m⁻³; <<http://modis.gsfc.nasa.gov/>>) and copepod biomass averaged over the period of 50 years (m⁻³, continuous plankton recorder (CPR), Sir Alistair Hardy Foundation for Ocean Science) were estimated at a resolution of 30 × 30 km (Fig. 1; see Supplementary material Appendix A1 for detailed methods). These environmental covariates are thought to be proxies for prey abundance and have been shown to be important predictors of foraging behaviour (Votier et al. 2010). We selected this spatial scale as the resolution of CPR data prohibits a finer resolution of copepod abundance being estimated. While fluctuations in SST and chl-a can be estimated on a finer temporal scale (Votier et al. 2010), there was incomplete coverage across our study area during the study period. Lower sea surface temperatures are typically associated with higher primary productivity (chlorophyll concentration; Fig. 1). Copepods feed on phytoplankton and as such there is a positive relationship between chlorophyll and copepod levels in our study system (Fig. 1). While the abundance and distribution of fish is unknown in this area, small fish which prey on copepods may be expected to have a positive relationship with copepod levels. The relationship between copepods and large piscivorous fish is unclear, as the spatial and temporal lag may lead to a mismatch between hotspots. As such, variation in the levels of these environmental covariates may demonstrate individual differences in prey choice. However, while we can predict the relationships between these environmental covariates, different oceanographic processes, temporal and spatial lags, and variation in diet among copepods and fish make the exact relationships very difficult to ascertain. All environmental covariates were population mean-centred to enable us to compare slopes among the population (van de Pol and Wright 2009).

Individual foraging consistency

First, we measured repeatability in foraging behaviour using seven variables. For each GPS track, we calculated: 1) trip duration (h), 2) total distance travelled (km), 3) departure angle from the colony (by averaging the first five bearings > 10 km from the colony to remove the influence of nest site location, degrees) and 4) the furthest location from the colony (longitude and latitude at terminal point). Using TDR dive data from Grassholm gannets we also determined, 5) maximum dive depth (m) and 6) dive profile shape, indicative of different foraging strategies (V shaped: bottom time < 3 s, U shaped: bottom time > 3 s; (Garthe et al. 2000) and by combining GPS and TDR data we estimated, 7) location of all dives. Grassholm GPS data was interpolated to a resolution of 1 s using a cubic spline interpolation to identify locations of dives and the environmental conditions at these sites extracted using ArcGIS 9.1. The repeatability (r) of each index and its associated standard error and p-value, testing the null hypothesis that between-group variance equals within-group variance, were estimated in the R package: rptR (Nakagawa and Schielzeth 2010). For departure angles, which are circular measures, bounded by 0 and 360, we used

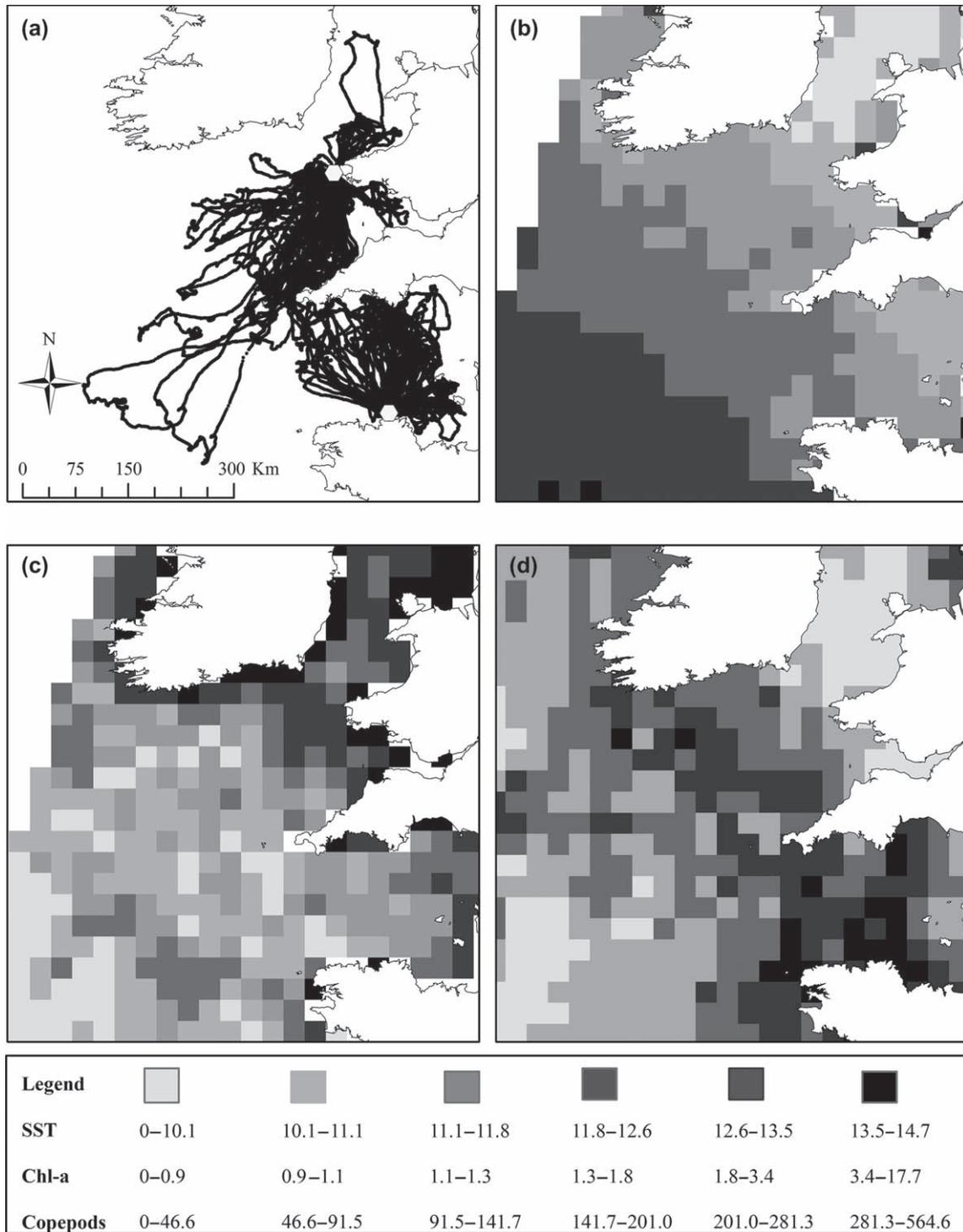


Figure 1. Movements and environmental conditions experienced by chick rearing northern gannets. (a) GPS tracks of adult gannets from Grassholm (18 birds, 66 tracks, July and August 2010) and Rouzic (13 birds, 51 tracks, June 2010); (b) sea surface temperature; (c) chlorophyll-a concentration; (d) average copepod biomass. Environmental variables are shown at a resolution of 30×30 km (white cells = no data).

a circular ANOVA (R package; circular) and calculated the repeatability using Lessells and Boag (1987) and their standard errors using Becker (1984). p-values are not available using this latter method. Individual colonies were analysed separately as they had different foraging ranges.

Second, we measured individual differences in the environmental conditions at dive sites. Every dive along

each foraging track was associated with a measure of SST, chl-a concentration and copepod biomass, to determine whether diving behaviour changed under different environmental conditions. The repeatability of each environmental covariate at the diving sites of an individual, and associated standard errors and p-values, was calculated using rptR (as above).

Individual search behaviour

When seabirds encounter a prey patch, they increase turning and slow down, which is associated with intensifying searching or prey intake (Pinaud and Weimerskirch 2007, Hamer et al. 2009). Previous work has shown that foraging sites can be inferred from GPS tracking data, by measuring these changes in turning and speed (Votier et al. 2010). Moreover, these measures can not only be used to highlight foraging areas, but can provide a continuous assessment of foraging intensity along foraging tracks. Using GPS tracks, we tested how changes in flight speed and path tortuosity of individual gannets varied with environmental conditions (see Measuring environmental gradients above). This was modelled using reaction norms, fitted in random slope mixed models (see Dingemanse et al. 2010 for more details). We modelled 1) straightness: the shortest straight line distance across a circle of 30 km, offset against the actual track length across the circle, fitted with a binomial error structure (see Supplementary material Appendix A1 for more details), 2) speed: the speed across a 30 km circle, fitted with a Gaussian error structure. We estimated the straightness and speed every two minutes along all foraging tracks. Individual bird identities were fitted as random slopes, that varied along SST, chl-a and copepod gradients simultaneously (see Box 4 in Dingemanse et al. 2010 for details on fitting reaction norms along multiple environmental gradients) and individual trip and bird were fitted as random intercepts. All environmental covariates and colony were included as fixed effects. We included a random effect with one level per observation (observational level random effect) to model the additive overdispersion in binomial models and fitted models using the lmer package in R (Bates and Maechler 2010).

As such, we fitted the general random intercept and slope model:

$$Y_{ij} \sim (\mu + \delta_i) + (\beta + \Delta_i)X_{ij} + e_{ij}$$

where: μ = population average intercept; δ_i = deviation from population average intercept for individual i ; β = population average slope; Δ_i = deviation from population average intercept for individual i ; e_{ij} = residual variation.

For analyses we fitted:

$$Y_{ijk} \sim (\mu + c + b_i + t_j) + (\beta_1 + \beta_2 + \beta_3 + \beta_{1_i} + \beta_{2_i} + \beta_{3_i}) \times X_{ijk} + e_{ijk}$$

where: i = individuals; j = observations grouped by individual trips; c = deviation from population intercept as a result of colony differences; b_i = deviation from population intercept as a result of variation between birds; t_j = deviation from population intercept as a result of variation between trips; e_{ijk} = residual variation; β_1 = population slope as a result of chlorophyll concentration; β_{1_i} = deviation from population average chlorophyll concentration for individual i ; β_2 = population slope as a result of SST; β_{2_i} = deviation from population average SST for individual i ; β_3 = population slope as a result of copepod concentration; β_{3_i} = deviation from population average copepod concentration for individual i .

The significance of variables was estimated by comparing models with and without the term of interest, using likelihood ratio tests (LRTs) where:

$$2\log(L_2/L_1) = 2[\log(L_2) - \log(L_1)]$$

where: L_1 = the likelihood of the full model; L_2 = the likelihood of the restricted model.

The LRT follows a χ^2 distribution, with the difference in the number of parameters between the models used as the number of degrees of freedom (Pinheiro and Bates 2000).

Model comparisons with different random effect structures were fitted using *REML* (restricted maximum likelihood) and those comparing models with different fixed effect structures were fitted using *ML* (maximum likelihood). While there are some concerns regarding the use of LRTs to test fixed effects in mixed models (Pinheiro and Bates 2000), these are thought to apply only to studies with small sample sizes (Fitzmaurice et al. 2004). In full models, an unstructured variance covariance matrix was fitted. However, to test for the significance of random effects, we constrained the covariance of the effect of interest to zero to ensure we tested the significance of the effect and not the combined significance of the effect and its covariance. The variation explained by each model was calculated using a Nagelkerke pseudo R^2 (Nagelkerke 1991), comparing the chosen model to a null model (with only a dummy random intercept). Random slopes were estimated using a full fixed effect structure. The estimates for fixed effects were extracted after removing non-significant random terms. All analyses were carried out in Matlab R2009b, R ver. 2.11.1 and ArcGIS ver. 9.3.

Results

Summary of data

On Grassholm, a total of 49902 GPS locations were collected from 18 individuals, along a total track length of 31553 km. We obtained three repeat trips from nine individuals, four repeats from eight individuals and six repeats from one individual. Individual track distances ranged from 77 km to 1782 km, travelling between 33 km and 472 km away from the colony with trip durations of 2.7 to 97.3 h (Fig. 1a). Dive data from 23 trips were collected from eight individuals. The deepest dive was 22.2 m and the longest lasted 37.5. From Rouzic, 58599 GPS locations were collected from 13 individuals, with a total distance of 21235 km travelled. We obtained two repeats from one individual, three repeats from two individuals, four repeats from seven individuals and five repeats from three individuals. The total distance travelled ranged from 68 km to 798 km with a maximum distance from the colony of 28 km to 193 km and trip durations from 14.4 to 46.5 h (Fig. 1a).

Individual foraging consistency

At both colonies, individuals consistently foraged along the same paths (Fig. 2) with highly repeatable terminal points (Grassholm: latitude $r = 0.54 \pm 0.13$; $p = 0.001$, longitude

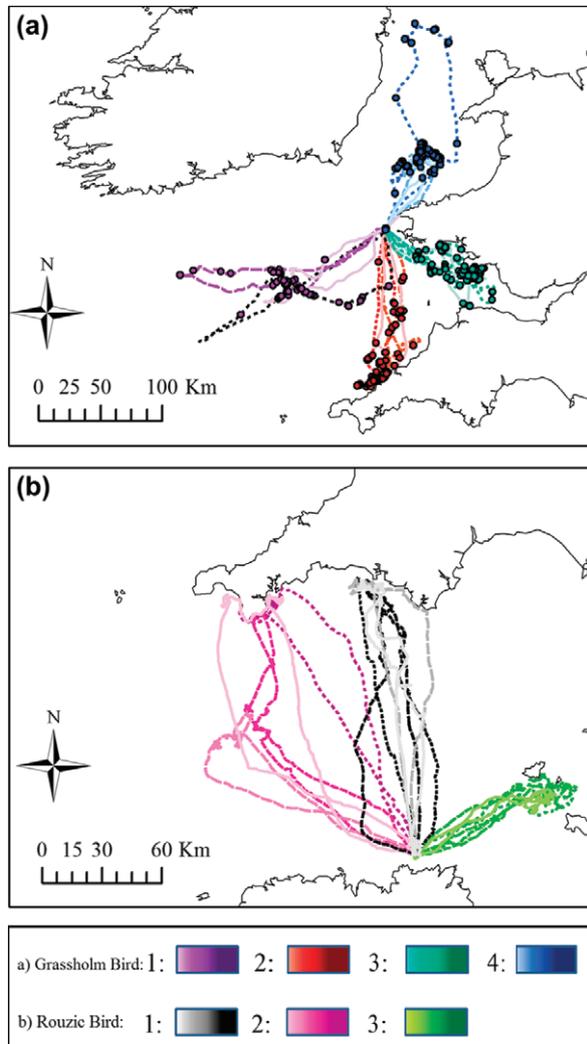


Figure 2. Specialisation in gannets. (a) Example repeat tracks and dives for four birds from Grassholm (3–4 tracks per bird) are shown. Individual birds and tracks are shown in different colours and shades respectively, with dives plotted as circles in the colour applicable to the track when they occurred. The colour gradient represents increasing track numbers: Pale colours (left of box) with solid lines are first tracks measured and dark tracks (right of box) with short-dashed line are last tracks measured. (b) Example repeat tracks are shown for four Rouzic birds (3–4 tracks per bird), colour coded as above. All birds show highly repeatable departure angles and foraging locations and Grassholm birds, repeatable dive sites. All tracks are sequential repeats, separated by the time a bird spent at the colony.

$r = 0.53 \pm 0.13$; $p = 0.008$; Rouzic: latitude $r = 0.57 \pm 0.15$; $p < 0.001$, longitude $r = 0.66 \pm 0.13$; $p < 0.001$ and departure angles (Grassholm: $r = 0.71 \pm 0.09$; Rouzic: $r = 0.55 \pm 0.14$). Individuals were not repeatable in trip duration (Grassholm: $r = 0.00 \pm 0.13$; $p = 0.70$; Rouzic: $r = 0.00 \pm 0.07$; $p = 0.79$) or total distance travelled (Grassholm: $r = 0.06 \pm 0.08$; $p = 0.26$; Rouzic: $r = 0.05 \pm 0.09$; $p = 0.25$).

At Grassholm, individual gannets showed both highly repeatable dive locations (latitude $r = 0.86 \pm 0.10$; $p < 0.001$, longitude $r = 0.84 \pm 0.10$; $p < 0.001$; Fig. 2) and environmental conditions at these sites (SST: $r = 0.46 \pm 0.14$; $p < 0.001$; chl-a: $r = 0.77 \pm 0.15$; $p < 0.001$; copepods:

$r = 0.76 \pm 0.13$; $p < 0.001$). Individual birds were much less repeatable in their maximum dive depths ($r = 0.18 \pm 0.07$; $p < 0.001$) and dive shape ($r = 0.18 \pm 0.08$; $p < 0.001$), although these metrics were still more significantly more repeatable than expected by chance.

Individual search behaviour

Gannet at-sea behaviour changed with environmental conditions and there was clear between-individual variation. Gannets altered their search behaviour differently according to copepods (straightness: $\chi^2_1 = 242.45$, $p < 0.001$; speed: $\chi^2_1 = 2695.5$, $p < 0.001$), chl-a (straightness: $\chi^2_1 = 517.15$, $p < 0.001$; speed: $\chi^2_1 = 4593.8$, $p < 0.001$) and SST (straightness: $\chi^2_1 = 10.34$, $p = 0.001$; speed: $\chi^2_1 = 2418.9$, $p < 0.001$; Table 1, Fig. 3). There were strong individual differences in the strength and direction of slopes demonstrating individual responses to environmental cues. Individuals with negative slopes increased searching with increasing SST, chl-a and copepods. Conversely individuals with positive slopes increased searching as SST, chl-a and copepods decreased. Straightness and speed models accounted for 50% and 55% of the data variance, respectively.

Discussion

Here we report novel aspects of foraging behaviour demonstrating that individual gannets show strongly consistent foraging behaviours and dive under consistently different environmental conditions. These results are strengthened by analyses showing that individuals also increased searching under different conditions. Together, these data suggest that spatial foraging consistency, reported here and elsewhere, may represent individual differences in preferred foraging habitat. Furthermore, individual responses to environmental gradients may provide a mechanism through which spatial foraging specialisation could arise.

Individual consistency and specialisation is predicted to be important as it acts to reduce intra-specific competition (Bolnick et al. 2003). This has previously been shown to occur through spatial partitioning, whereby individuals forage in different locations or at different depths (Supplementary material Appendix A1 Table A1). Here we show further evidence of consistently divergent space use between individual gannets, and that this is tightly linked to consistent departure angles from the colony (see also Pettex et al. 2010). While this spatial segregation limits individual overlap in foraging area, it reveals little information on individual dietary segregation. Results from stable isotope analysis suggest that individuals forage on different prey types and that this variation persists over time (Votier et al. 2010). Here, using high resolution GPS tracking data, we link these two findings, demonstrating that spatial segregation is associated with differences in environmental conditions at foraging sites. As environmental variables are thought to be good proxies for prey type and abundance (Votier et al. 2010), our findings provide support for individual dietary specialisation.

Given that predators should increase their searching intensity before encountering a prey patch (Pinaud and Weim-

Table 1. The results of models estimating the individual straightness and speed response to environmental covariates. Random slopes were estimated using a full fixed effect structure. Non-significant random slopes were dropped from the model to test the significance of fixed effect terms.

	Variables sample size	Tortuosity	Speed
		data points = 43 443; tracks = 113; birds = 31	
Random slopes	copepods	$\chi_1 = 242.45$; $p < 0.001$	$\chi_1 = 2695.5$; $p < 0.001$
	chlorophyll	$\chi_1 = 517.15$; $p < 0.001$	$\chi_1 = 4593.8$; $p < 0.001$
	sea surface temperature	$\chi_1 = 10.34$; $p = 0.001$	$\chi_1 = 2418.9$; $p < 0.001$
Random intercepts	individual bird	$\chi_1 = 4.4$; $p = 0.04$	$\chi_1 = 146.0$; $p < 0.001$
	individual track	$\chi_1 = 1364.3$; $p < 0.001$	$\chi_1 = 9779.6$; $p < 0.001$
	colony	$\chi_1 = 13.12$; $p < 0.001$; Grassholm: -1.49 ± 0.15 Rouzic: -1.09 ± 0.22	$\chi_1 = 1.57$; $p = 0.21$
Fixed effects	copepods	$\chi_1 = 12.46$; $p < 0.001$; estimate: 0.007 ± 0.002	$\chi_1 = 5.57$; $p = 0.02$; estimate: 0.36 ± 0.001
	chlorophyll	$\chi_1 = 0.40$; $p = 0.52$	$\chi_1 = 0.44$; $p = 0.51$
	sea surface temperature	$\chi_1 = 0.00$; $p = 1.00$	$\chi_1 = 1.36$; $p = 0.24$

erskirch 2007, Hamer et al. 2009), individual differences in foraging conditions should be coupled with individual differences in searching response along these gradients. Our results provide the first support for this hypothesis, demonstrating that individuals increase their searching intensity under different environmental conditions. These results together indicate that the consistent differences in foraging behaviour exhibited here and reported elsewhere may be maintained by, or may even have arisen as a consequence of, variation in individual responses to environmental gradients, driving diversification and consistency across large spatial scales. Given the short term nature of our study, we can not exclude that these consistent behaviours occur as a result of highly successful foraging grounds being repeatedly exploited and that individuals change behaviour when unsuccessful. While this seems unlikely across the population, longer term and

between year comparisons would be able to exclude success as a driver of consistency.

By using population mean centred environmental covariates, we calculate a measure of plasticity in searching behaviour associated with habitat choice (van de Pol and Wright 2009, Dingemanse et al. 2010). However recent work has suggested that these two components can be partitioned, isolating non-random association with environmental conditions and plasticity in searching response simultaneously (Dingemanse and Dochtermann 2013). As bio-logging continues to become cheaper and data sets build over time, sufficient data should exist to examine these components separately. Some definitions of foraging specialisation involve an element of constraint on behaviour (Bolnick et al. 2003) and reaction norms, used across time and contexts, could assess whether these behaviours are restricted within individuals.

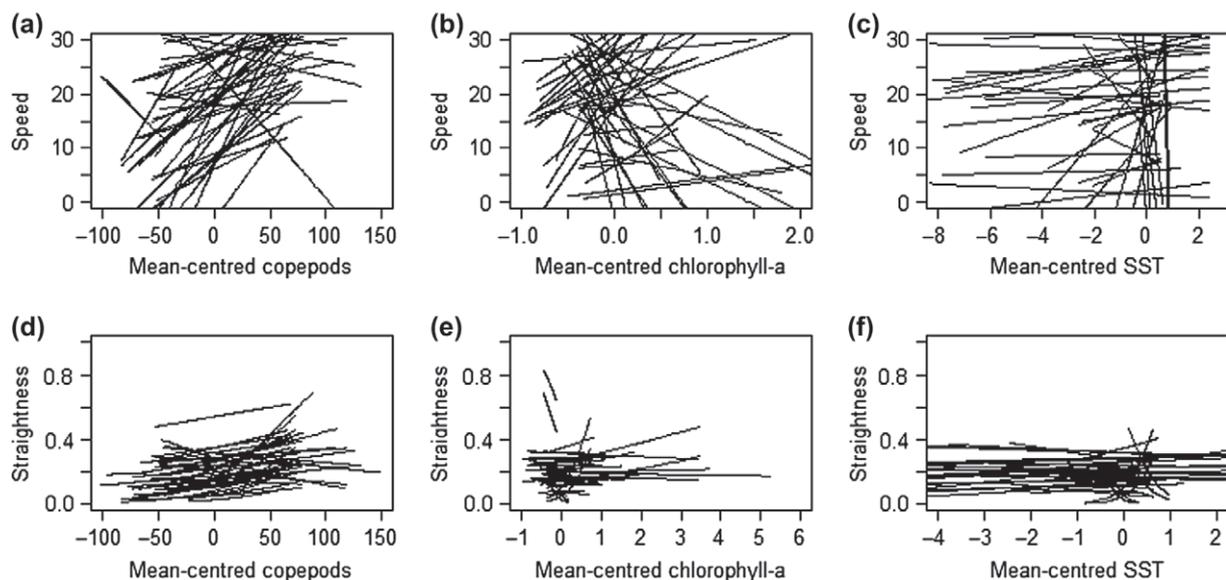


Figure 3. Individual changes in searching in response to environmental gradients. Each slope shows an individual gannet's search response to a mean centred (standardised) environmental gradient and these plots highlight the variation in direction and strength of slope between individuals, providing evidence that individuals intensify searching under different conditions. (a) Variation in individual speed response to copepod biomass. (b) Variation in individual speed response to chl-a. (c) Variation in individual speed response to SST. (d) Variation in individual path straightness response to copepod biomass. (e) Variation in individual path straightness response to chl-a. (f) Variation in individual path straightness in response to SST.

We also report much less repeatable behaviours, such as trip duration and total distance travelled, suggesting that birds use different routes to arrive at foraging sites. Previous studies have also reported individual variability in certain behaviours, and it has been suggested that this flexibility allows birds to adapt to changing oceanographic or biological pressures (Weimerskirch et al. 1993, Iverson and Esler 2006, Gremillet and Boulinier 2009, Votier et al. 2013). Fine scale changes in weather conditions are likely to influence the most efficient route to foraging sites, and we suggest this may account for some within-individual variation in trip duration and length. While learning and memory effects have been suggested to be important in locating foraging grounds, evidence that individuals use different routes to repeatedly forage at the same location suggests that individual assessment of environmental variables is likely to be important.

While we show individual differences in response to environmental variables, it is still unclear what sensory cues birds are using to assess the environment. There is evidence that Procellariiformes (Nevitt et al. 2008, Mardon et al. 2010) and penguins (Wright et al. 2011) use olfaction to locate their prey, and differences in environmental gradients could potentially lead to differences in the odour landscape at sea. However there is currently no evidence for individual differences in olfactory responses and the fused nostrils of gannets suggest that odour is unlikely to facilitate prey capture. Differences in small scale tidal structures or phytoplankton blooms are potentially conspicuous visual cues (Tew Kai et al. 2009), but more work is required to determine whether such features are relevant for searching gannets and other marine predators. Furthermore, the exact relationships between environmental covariates and prey abundance and diversity are lacking but work combining trophic markers such as stable isotopes with habitat preferences may be able to clarify these patterns in the future.

This study presents consistent results from two colonies, in different water masses. Given the variation in timing of breeding, oceanographic conditions and anthropogenic pressures (e.g. fishing intensity), the similarities between colonies suggest a generality in our results. We demonstrate a high degree of individual foraging consistency among central place breeding gannets. We show that individual gannets consistently differ in their at-sea movements along environmental gradients, and this intra-population variation in search behaviour may result in repeated use of different foraging locations. Therefore, we believe these individual-level responses to environmental variables in marine ecosystems may play an important role in the origin and maintenance of foraging specialisations over very large spatial scales. Moreover, we suggest that inter-individual differences in search response to environmental cues offer a plausible underlying behavioural mechanism for widely reported individual foraging specialisations among marine vertebrates and beyond.

Acknowledgements – Thanks to the RSPB and Greg and Lisa Morgan for access to Grassholm and help in the field with Claudia Strauss, James Waggitt and Dave Evans and logistic support from Tim Brooke (Venturejet). Thanks all staff at LPO Ile Grande, for help in the field and logistical support. Copepod biomass data

was provided by the Sir Alexander Hardy Foundation for Ocean Science and thanks to David Johns for data assistance. Thanks also to Tim Guilford, Robin Freeman, Holly Kirk, Ben Dean, Niels Dingemanse, Dave Hodgson, Shinichi Nakagawa, Charlie Cornwallis, Matthieu Authier, Dionysis Raitsos, Rich Inger, Dan Buscombe, Luca Borger and Xav Harrison, for helpful discussions. Julien Martin and Ben Chapman provided very valuable comments which greatly improved the manuscript. Funding was provided by the EU Interreg CHARM III project, NERC (NE/H007199/1, NE/G001014/1 and NE/H007466/1), the Peninsula Research Institute for Marine Renewable Energy, the Centre d'Ecologie Fonctionnelle et Evolutive at CNRS Montpellier, the EU Interreg FAME project (co-funded by ERDF, Agence des aires marines protégées and LPO) and a Marie Curie Intra-European Fellowship to S. Patrick.

References

- Araujo, M. S. et al. 2007. Using delta C-13 stable isotopes to quantify individual-level diet variation. – *Oecologia* 152: 643–654.
- Bates, D. and Maechler, M. 2010. lme4: linear mixed-effects models using Eigen and Eigen. – R package ver. 0.999375-35.
- Becker, W. A. 1984. A manual of quantitative genetics. – Academic Enterprises.
- Bolnick, D. I. et al. 2003. The ecology of individuals: Incidence and implications of individual specialization. – *Am. Nat.* 161: 1–28.
- Dingemanse, N. J. and Dochtermann, N. A. 2013. Quantifying individual variation in behaviour: mixed effect modelling approaches. – *J. Anim. Ecol.* 82: 39–54.
- Dingemanse, N. J. et al. 2010. Behavioural reaction norms: animal personality meets individual plasticity. – *Trends Ecol. Evol.* 25: 81–89.
- Fitzmaurice, G. et al. 2004. Applied longitudinal analysis. – Wiley.
- Garthe, S. et al. 2000. Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). – *Proc. R. Soc. B* 267: 1717–1722.
- Garthe, S. et al. 2007. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. – *Mar. Biol.* 151: 687–694.
- Gremillet, D. and Boulinier, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. – *Mar. Ecol. Progr. Ser.* 391: 121–137.
- Gremillet, D. and Charmantier, A. 2010. Shifts in phenotypic plasticity constrain the value of seabirds as ecological indicators of marine ecosystems. – *Ecol. Appl.* 20: 1498–1503.
- Hamer, K. C. et al. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. – *Mar. Ecol. Progr. Ser.* 338: 295–305.
- Hamer, K. C. et al. 2009. Fine-scale foraging behaviour of a medium-ranging marine predator. – *J. Anim. Ecol.* 78: 880–889.
- Iverson, S. A. and Esler, D. 2006. Site fidelity and the demographic implications of winter movements by a migratory bird, the harlequin duck *Histrionicus histrionicus*. – *J. Avian Biol.* 37: 219–228.
- Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities – a common mistake. – *Auk* 104: 116–121.
- Mardon, J. et al. 2010. Insight of scent: experimental evidence of olfactory capabilities in the wandering albatross (*Diomedea exulans*). – *J. Exp. Biol.* 213: 558–563.
- Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. – *Biometrika* 78: 691–692.

- Nakagawa, S. and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. – *Biol. Rev.* 85: 935–956.
- Nevitt, G. A. et al. 2008. Evidence for olfactory search in wandering albatross, *Diomedea exulans*. – *Proc. Natl Acad. Sci. USA* 105: 4576–4581.
- Nussey, D. H. et al. 2005. Selection on heritable phenotypic plasticity in a wild bird population. – *Science* 310: 304–306.
- Pettex, E. et al. 2010. Northern gannets anticipate the spatio-temporal occurrence of their prey. – *J. Exp. Biol.* 213: 2365–2371.
- Pinaud, D. and Weimerskirch, H. 2005. Scale-dependent habitat use in a long-ranging central place predator. – *J. Anim. Ecol.* 74: 852–863.
- Pinaud, D. and Weimerskirch, H. 2007. At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. – *J. Anim. Ecol.* 76: 9–19.
- Pinheiro, J. and Bates, D. 2000. *Mixed-effects models in S and S-PLUS*. – Springer.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism – a review of the evidence. – *Q. Rev. Biol.* 64: 419–461.
- Shine, R. 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. – *Am. Nat.* 138: 103–122.
- Tew Kai, E. et al. 2009. Top marine predators track Lagrangian coherent structures. – *Proc. Natl Acad. Sci. USA* 106: 8245–8250.
- van de Pol, M. V. and Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. – *Anim. Behav.* 77: 753–758.
- van de Pol, M. K. et al. 2009. Using oystercatchers' bill shapes as a proxy for feeding specialization: more differentiation than meets the eye? – *Ardea* 97: 335–347.
- Votier, S. C. et al. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. – *J. Appl. Ecol.* 47: 487–497.
- Votier, S. C. et al. 2013. A bird's eye view of discard reforms: bird-borne cameras reveal seabird/ fishery interactions. – *PLoS ONE* 8: e57376.
- Wanless, S. et al. 2008. Later breeding in northern gannets in the eastern Atlantic. – *Mar. Ecol. Progr. Ser.* 370: 263–269.
- Weimerskirch, H. et al. 1993. Foraging strategy of wandering albatrosses through the breeding-season – a study using satellite telemetry. – *Auk* 110: 325–342.
- Weimerskirch, H. et al. 2007. Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. – *Am. Nat.* 170: 734–743.
- Wilson, R. P. et al. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. – *Mar. Ecol. Progr. Ser.* 228: 241–261.
- Wright, K. L. B. et al. 2011. Penguins are attracted to dimethyl sulphide at sea. – *J. Exp. Biol.* 214: 2509–2511.

Supplementary material (available online as Appendix oik-00406 at www.oikosoffice.lu.se). Appendix A1: Table A1. Individual foraging specialisation has been demonstrated in a wide-range of air-breathing marine vertebrates. Appendix A2: Additional methods and analysis details. Table A2 and A3. The correlations between all foraging and dive parameters from the Grassholm colony (A2) and Rouzic (A3). Figure A1. A schematic diagram demonstrating how path straightness was calculated.