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1 **Long-term individual foraging site fidelity – why some gannets don't change their spots**

2

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14

15 **Abstract**

16 Many established models of animal foraging assume that individuals are ecologically equivalent.

17 However, it is increasingly recognized that some populations comprise animals whose diets and

18 foraging behaviours differ consistently among individuals. For example, recent studies have

19 shown that individual foraging site fidelity (IFSF - when individuals consistently forage in only a

20 small part of their population's home range) occurs in some colonial breeders. Short-term IFSF

21 could result from animals using a win-stay, lose-shift (WSLS) foraging strategy. Alternatively, it

22 may be a consequence of other forms of individual specialisation. Pelagic seabirds are colonial

23 central-place foragers, classically assumed to use flexible foraging strategies to target widely

24 dispersed, spatiotemporally patchy prey. However, tracking has shown that IFSF occurs in many
25 seabirds, although it is not known whether this persists across years. To test for long-term IFSF
26 and to examine alternative hypotheses concerning its cause, we repeatedly tracked 55 northern
27 gannets from a large colony in the North Sea within and across three successive breeding
28 seasons. Gannets foraged in neritic waters, predictably structured by tidal mixing and thermal
29 stratification but subject to stochastic wind-induced overturning. Both within and across years,
30 coarse to mesoscale (10s km) IFSF was significant but not absolute and foraging birds departed
31 the colony in individually consistent directions. Carbon stable isotope ratios in gannet blood
32 tissues were repeatable within years and nitrogen ratios were also repeatable across years,
33 suggesting long-term individual dietary specialisation. Individuals were also consistent across
34 years in habitat use with respect to relative sea surface temperature and in some dive metrics yet
35 none of these factors accounted for IFSF. Moreover, at the scale of weeks, IFSF did not decay
36 over time and the magnitude of IFSF across years was similar to that within years, suggesting
37 that IFSF is not primarily the result of WSLs foraging. Rather, we hypothesise that site
38 familiarity, accrued early in life, causes IFSF by canalising subsequent foraging decisions.
39 Evidence from this and other studies suggests that IFSF may be common in colonial central-
40 place foragers, with far-reaching consequences for our attempts to understand and conserve these
41 animals in a rapidly changing environment.

42

43 **Keywords:** Site familiarity, individual specialisation, niche partitioning, gannet, *Morus*
44 *bassanus*, GPS tracking, central-place forager, tidal mixing front.

45

46

47 **Introduction**

48 An assumption implicit to many established theories of animal habitat selection, such as the ideal
49 free and ideal despotic models (Fretwell and Lucas 1969), is that individuals are ecologically
50 equivalent (Piper 2011). Hence, the increasing realisation that behaviour in many animal
51 populations differs consistently among phenotypically similar individuals has far reaching
52 implications for ecology, evolution and wildlife management (Bolnick et al. 2003, Piper 2011,
53 Dall et al. 2012). Site fidelity (when an animal repeatedly uses the same location) is a common
54 form of individual behavioural consistency (Switzer 1993, Piper 2011). For example, birds
55 frequently return each year to the same breeding territory or wintering area (Phillips et al. 2005,
56 Piper 2011). Similarly, individual foraging site fidelity (IFSF) occurs when within-individual
57 variation in the use of space during foraging is less than that across the population as a whole. As
58 such, IFSF could be regarded as a form of individual specialisation (Bolnick et al. 2003, Patrick
59 et al. 2014). However, IFSF could be either a cause or a consequence of other types of
60 specialisation (e.g. in diet, behaviour, habitat, etc.) (Woo et al. 2008, Beverly et al. 2009) or it
61 could have other, unrelated, proximate causes (Piper 2011). In colonial animals, theory suggests
62 that the individual behaviour is influenced by that of the group (Ward and Zahavi 1973). It is
63 perhaps surprising therefore that recent studies have shown IFSF in breeding seabirds and other
64 colonial central-place foragers, including pinnipeds, bats and ants (Kerth et al. 2001,
65 Weimerskirch 2007, Beverly et al. 2009, Baylis et al. 2012). Although individual dietary and
66 behavioural specialisation is frequent in seabirds (Patrick et al. 2014), there is little evidence on
67 the causal relationships between these phenomena and IFSF. Moreover, it is unknown whether
68 IFSF in seabirds persists across breeding seasons (Weimerskirch 2007).

69

70 IFSF could also be a consequence of search behaviour. In a spatiotemporally patchy
71 environment, foragers may employ a win-stay, lose-shift (WSLS) strategy (Kamil 1983, Davoren
72 et al. 2003). If this were the case, IFSF would continue only for as long as prey patches persisted
73 but would ultimately decay over time. Classically, pelagic seabirds were assumed to forage on
74 highly patchy and unpredictable resources, making them necessarily flexible foragers, reliant
75 largely on searching or public information gain, rather than memory, to locate their prey (Lack
76 1968, Ward and Zahavi 1973). However, recent observations that IFSF within breeding seasons
77 is high, and that birds travel directly to foraging areas, rather than following sinuous search
78 paths, has been regarded as evidence that the occurrence of prey (in temperate and polar seas at
79 least) is predictable at the coarse- to mesoscale (10s – 100s km) and over days and weeks (Irons
80 1998, Weimerskirch 2007). However, the swarming species upon which seabirds principally
81 prey are likely distributed in a hierarchical patch system, in which predictability reduces with
82 decreasing spatiotemporal scale (Fauchald and Tveraa 2006). This is evinced by the fact that
83 some species use nested area restricted search (ARS) patterns, the scale of which is matched to
84 that of habitat structures (Pinaud and Weimerskirch 2005, Hamer et al. 2009). Moreover, seabird
85 breeding success, which is dependent largely on food supply, varies markedly between years
86 (Cury et al. 2011). As such, it may be advantageous for seabirds to maintain sufficient
87 behavioural plasticity to respond to environmental stochasticity, for example by using public
88 information to locate new prey patches and private information (memory) to relocate them
89 (Ward and Zahavi 1973, Weimerskirch et al. 2010, Wakefield et al. 2013). Hence, if IFSF is
90 attributable to WSLS foraging, then its rate might be expected to match the scale of
91 environmental variability and decay over time. Moreover, if repeatability in diet, habitat choice
92 and prey capture method are consequences rather than causes of IFSF, then individual

93 specialisations might also be expected to decay over time. This prediction is consistent with the
94 observation that rates of behavioural repeatability tend to be higher when observations are
95 closely spaced (Woo et al. 2008, Bell et al. 2009) but contrary to the observation that individual
96 dietary specialisations persist over inter-annual scales in some wide-ranging higher marine
97 predators (Matich et al. 2011, Vander Zanden et al. 2013).

98

99 Irons (1998) suggested an alternative cause of IFSF: site familiarity. That is, by maintaining
100 foraging site fidelity seabirds acquire information specific to that site, such as local tidal features,
101 conferring a competitive advantage (the ‘always stay’ strategy (Switzer 1993)). Until recently
102 site familiarity has received little attention yet it may play an important role in habitat selection
103 by making animals more spatially conservative with experience (Piper 2011). If seabirds’
104 foraging decisions are affected by site familiarity then IFSF may persist across breeding seasons.
105 Inter-annual IFSF has been recorded in breeding pinnipeds (Bradshaw et al. 2004, Call et al.
106 2008). However, to our knowledge, no previous studies have tested for it in breeding seabirds or
107 examined the relationship between IFSF and other forms of individual behavioural consistency at
108 this scale (Weimerskirch 2007, Patrick et al. 2014). Moreover, the fitness consequences of IFSF
109 and individual specialisation are far from clear (Woo et al. 2008).

110

111 Northern gannets *Morus Bassanus* (hereafter gannets) are large pelagic seabirds that breed on
112 temperate to low-Arctic coasts of the North Atlantic (Nelson 2001). They range up to 100s km
113 from their colonies to forage almost exclusively in neritic waters (Hamer et al. 2000, Garthe et
114 al. 2011, Wakefield et al. 2013). Breeding individuals tracked for up to 3 weeks show significant
115 but not absolute IFSF (Hamer et al. 2001, Patrick et al. 2014). Moreover, they tend to follow

116 highly directed paths from their colonies, supporting the hypothesis that they anticipate the
117 location of their prey at the timescale of days-weeks and scales of 10s to 100s of km (Pettex et al.
118 2010). However, at finer scales (10s km) they also use ARS, which is characterised by a tortuous
119 flight path (Fauchald and Tveraa 2006), to locate prey, though it is not known whether the scale
120 of ARS reflects that of prey patches or underlying habitat structures (Hamer et al. 2009). At these
121 scales they also gain information on prey distribution from observing foraging conspecifics
122 (local enhancement) (Camphuysen 2011) and may be attracted to fishing vessels, from which
123 some individuals obtain large quantities of discards (Votier et al. 2010, Bodey et al. 2014).
124 Gannets capture prey by diving, following either V or U-shaped profiles depending on prey type
125 (Garthe et al. 2000). Blood tissue stable isotope ratios indicate that individuals are short-term
126 dietary specialists (Kakela et al. 2007, Votier et al. 2010), while consistent differences in
127 individual behavioural responses to sea surface temperature (SST), chlorophyll-a and copepod
128 abundance have been interpreted as evidence of site specialisation (Patrick et al. 2014).
129
130 Gannets breeding at the Bass Rock in the North Sea, one of the world's largest colonies (~60,000
131 breeding pairs), forage in habitats that are predictably structured at the coarse to mesoscale (10s
132 – 100s km) by the tide and seasonal thermal stratification (Fig. 1). Shallower waters remain
133 mixed due to tidal stirring, with tidal mixing fronts forming at the interface of these two regimes
134 (Simpson 1981). Such tidally forced dynamics are very predictable. However, both seasonal
135 stratification and the location of mixing fronts is subject to modification by wind-induced
136 overturning, which is episodic and unpredictable within breeding seasons, and tracking data
137 show that population level home ranges can vary considerably across years, presumably in
138 response to variability in prey availability (Hamer et al. 2007).

139

140 Despite this wealth of information, it is not known whether IFSF occurs across breeding seasons
141 or whether individual specialisations persist at this scale. The aims of our study were therefore,
142 first, to determine whether IFSF in a colonial central-place forager inhabiting a patchy but semi-
143 predictable environment persists over long time scales and, second, to examine the potential
144 causes of IFSF. By repeatedly tracking and blood-sampling the same individual gannets from
145 Bass Rock within successive breeding seasons we tested (at the scale of weeks and years) the
146 hypotheses that IFSF: (1) is significant and dependent on consistency in diet, foraging behaviour
147 or habitat use; (2) decays over time; (3) varies with the directedness of trips, and; (4) affects
148 individual body condition.

149

150 **Materials and Methods**

151 *Study design and data collection*

152 Fieldwork was conducted on Bass Rock (56° 6'N, 2° 36'W, Fig. 1) from June - August, 2010 –
153 2012, during which time we collected blood samples from adult gannets and tracked their
154 movements over successive foraging trips. We aimed firstly to estimate individual consistency
155 (defined below) in the use of space and habitat in a comparable manner within years and across
156 years. We therefore aimed to track birds for a minimum of three foraging trips within each of
157 three consecutive breeding seasons. In the event, we were able to track some birds for > three
158 trips within years (see Results). Where possible, we analysed these additional data using
159 hierarchical models.

160

161 Birds of unknown age were caught at the nest, while they were attending 2 - 5 weeks old chicks,
162 using a metal crook or brass wire noose fitted to a 4-6 m telescopic pole, and restrained in a
163 custom-made jacket. Time permitting, on initial capture we measured culmen length (tip to
164 feathering) and maximum tarsus length (± 1 mm) using a Vernier calliper. On first capture within
165 each year, y (time $t_{y,1}$), after birds had fed their chicks, we also measured body mass to the
166 nearest 25 g using a 5 kg spring balance. We then attached an Igotu GT-200 or GT-600 (Mobile
167 Action Technology Inc., Taipei, Taiwan, 37 g) Global Positioning System (GPS) logger to the
168 dorsal side of the central three tail feathers using Tesa tape. GPS units sampled position at 2
169 minute resolution. In addition, in 2011 and 2012, we fitted some birds with a Time Depth
170 Recorder (TDR; either a G5, CEFAS Technology, Lowestoft, UK or MSR145, MSR Electronics
171 GmbH, Seuzach, Switzerland, 2.5 g and 18 g respectively). Birds were recaptured (time $t_{y,2}$), and
172 loggers removed after 1 – 3 weeks. Total instrument mass was $\leq 2\%$ of body mass, below the
173 maximum recommended for bio-logging studies (Phillips et al. 2003). After release, birds
174 returned almost immediately to the nest, and devices had no discernible effects on birds' trip
175 durations (Cleasby et al. in press).

176

177 At both $t_{y,1}$ and $t_{y,2}$ we collected ~ 0.8 ml of blood from the tarsal vein of each gannet using a 23
178 gauge needle (under a UK Home Office licence). Within an hour, we centrifuged samples at
179 15,000 rpm for 10 minutes to separate plasma and erythrocytes, which were then stored frozen.
180 In addition, we retained 0.2 ml of whole blood from each bird, which we stored in 98% ethanol
181 for molecular sex determination, which was carried out at the Natural Environment Research
182 Council (NERC) Biomolecular Analysis Facility, Sheffield. Throughout the study, we collected,

183 identified and stored prey spontaneously regurgitated by adult gannets during handling to assess
184 their diet (Votier et al. 2010).

185

186 To describe the distribution and consistency of individual foraging effort with respect to habitat,
187 we considered environmental variables known to influence the distribution of foraging gannets
188 or their prey. These variables, and our rationale for selecting them, were: (i) Distance from
189 colony: The energetic and temporal costs of foraging as well as the intensity of intraspecific
190 competition vary with distance from the colony (Wakefield et al. 2013); (ii) depth and (iii) slope
191 of seafloor: Gannets sometimes forage over relatively shallow offshore banks, which are an
192 important habitat for sandeels *Ammodytes* spp., which comprise up to half of the biomass in the
193 diet of gannets at Bass Rock in some years (Hamer et al. 2007), as well as areas of steep
194 bathymetric relief (Hamer et al. 2001, Scott et al. 2010); (iv) fishing effort: Fishery discards
195 comprise ~ 10 – 30 % of the diet of gannets in UK waters (Hamer et al. 2007, Kakela et al. 2007,
196 Votier et al. 2010) and foraging gannets are attracted to fishing vessels (Votier et al. 2010,
197 Camphuysen 2011, Bodey et al. 2014); (v) SST and (vi) relative front density (Miller 2009): In
198 shallow, tidally dominated seas, SST discriminates thermally stratified (warm) from tidally
199 mixed (cool) waters (Simpson 1981). The density of foraging gannets varies systematically with
200 SST (Scott et al. 2010) and increases in the vicinity of tidal mixing fronts between cool and
201 mixed waters (Hamer et al. 2009); (vii) Net Primary Production (NPP): The distribution of
202 mesotrophic fish that gannets prey upon (e.g. mackerel *Scomber scombrus* and herring *Clupea*
203 *harengus*) is partly limited by lower trophic level organisms, for which NPP is a proxy. The
204 density of foraging gannets therefore tends to increase with primary production (Grémillet et al.

205 2008, Scott et al. 2010, Votier et al. 2010). For sources and pre-processing of environmental data
206 see Appendix A.

207

208 *Quantifying repeatability*

209 Individual consistency in continuous measures of behaviour or diet may be quantified using the
210 repeatability, R , where

211

$$212 \quad R = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\varepsilon}^2}, \quad (1)$$

213

214 and σ_{α}^2 and σ_{ε}^2 is the variance between- and within individuals respectively. This index and its
215 implementation are discussed at length by Nakagawa and Schielzeth (2010). The variance
216 components in eq. 1 may be estimated using linear mixed-effects models of the variable of
217 interest as a function of animal identity, which is specified as a random effect. Other explanatory
218 terms (e.g. sex, age, etc.) can be included as fixed effects. In this case, Nakagawa and Schielzeth
219 (2010) use the term adjusted repeatability R_{adj} because controlling for fixed effects will affect
220 the variance component (and hence repeatability) estimates in equation 1. By implementing these
221 models in a Bayesian framework, posterior estimates can be used to calculate credibility intervals
222 around R_{adj} . Following this approach, we used the R package MCMCglmm (Hadfield 2010) to
223 model behavioural and dietary indices using generalised linear mixed-effects models (GLMM)
224 fitted to all trip data. We simplified models by backward-selection, minimising the Deviance
225 Information Criterion (DIC (Claeskens and Hjort 2008)) and retaining fixed effects only if their
226 removal resulted in an increase in DIC of 5 or more (Lunn et al. 2012).

227 In order to examine the relationship between individual repeatability and other covariates we
228 also calculated the individual-level adjusted repeatability for each bird:

229

$$230 \quad R'_{adj,i} = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_i^2}, \quad (2)$$

231

232 where σ_{α}^2 is the between-individual residual variance component and σ_i^2 is the residual variance
233 for the i th individual, estimated by the minimum adequate model.

234

235 *Isotopic repeatability*

236 In order to estimate individual dietary repeatability (hypothesis 1), we used the ratios of stable
237 isotopes of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) in the blood tissues of birds (expressed as
238 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively) as proxies for diet (Appendix B for further details). $\delta^{15}\text{N}$ values vary
239 with the trophic position of prey and $\delta^{13}\text{C}$ values with water mass, depth and distance from land
240 (Hobson et al. 1994, Cherel and Hobson 2007). Due to their different turnover rates, body tissues
241 integrate diet at different time scales. The half-lives of both stable isotope ratios in avian blood
242 plasma (PLA) and red-blood cells (RBC) range from approximately 1 - 8 days and 14 - 30 days,
243 respectively (Barquete et al. 2013). The repeatability of stable isotope ratios in different tissues
244 collected from an individual at the same time or the same tissues collected at different times is
245 therefore a proxy for individual dietary specialization (Bearhop et al. 2006, Matich et al. 2011).
246 Accordingly, blood samples were collected from each gannet at $t_{y,1}$ and $t_{y,2}$ and separated into
247 plasma and erythrocytes, if possible, in each study year. Sex was determined using molecular

248 methods. Prey and gannet tissue samples were prepared following standard procedures and stable
249 isotope ratios measured by continuous flow mass spectrometry (Appendix B for details).

250

251 We estimated R_{adj} and R'_{adj} for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the blood tissues of gannets, within and across
252 years. Within each year, we modelled isotopic ratios in RBC and PLA sampled at $t_{y,1}$, and PLA
253 sampled at $t_{y,2}$ as repeated measures. Across years, we modelled isotopic ratios in RBC sampled
254 at $t_{y,1}$ in each year. Exploratory data analysis showed stable isotope values to be approximately
255 normally distributed. We considered the following candidate fixed effects: (i) sex (diet, spatial
256 usage and foraging behaviour of male and female gannets differ (Lewis et al. 2002, Stauss et al.
257 2012, Cleasby et al. in press)); (ii) tissue type (enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tends to differ
258 systematically with tissue type (Zhao et al. 2006)); (iii) environmental baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
259 (Jennings and Warr 2003, Barnes et al. 2009). (In the marine environment, differing rates of
260 primary productivity can result in spatial variation in baseline stable isotope ratios (Moreno et al.
261 2011). Baseline $\delta^{15}\text{N}$ is 2 to 2.5 ‰ higher in the permanently mixed waters of the southern North
262 Sea than in the northern sector (Fig. 2 in Jennings and Warr 2003), while that of $\delta^{13}\text{C}$ is 0.5 to 1
263 ‰ higher (Fig. 2 in Barnes et al. 2009). In addition, $\delta^{13}\text{C}$ decreases with distance from the coast.
264 Hence, repeatability in gannet tissue isotopic ratios may reflect not only dietary repeatability but
265 spatial consistency.); (iv) year (baseline stable isotope ratios may change from year to year
266 (Moreno et al. 2011)). Random effects allowed for among-individual variation in intercepts the
267 response baseline stable isotope ratios.

268

269 We obtained baseline estimates of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from isoscapes predicted by models fitted to
270 tissue isotope ratios measured in phytoplankton-feeding bivalve molluscs (*Aequipecten*

271 *opercularis*) sampled throughout the North Sea (Jennings and Warr 2003, Barnes et al. 2009).
272 We digitised isoscapes presented in these publications and appended baseline ratios to each
273 tracking location. For each bird, we then calculated the median baseline isotopic ratio across all
274 putative foraging locations within each year (Appendix B for details).

275

276 ***Behavioural repeatability***

277 To test hypotheses 1 and 4, we summarised individual foraging behaviour by trip using the
278 following indices (Appendix C for details): daylight trip duration, assuming that this reflects
279 available foraging time; median foraging range; ARS scale (i.e. the scale at which variance in the
280 first-passage time peaked (Pinaud and Weimerskirch 2005)). For birds equipped with TDRs we
281 also calculated the mean dive depth, mean maximum dive depth, dive rate, and the proportion of
282 V shaped dives (dives were classified as either V-shaped or U-shaped), all of which potentially
283 reflect individual differences in foraging strategies, prey types or habitat use (Garthe et al. 2000,
284 Woo et al. 2008). We estimated R_{adj} and R'_{adj} of these indices by treating trips as individual-
285 level repeated measures, within or across years and considering sex and in the latter case, year,
286 as candidate fixed effects. We \log_e -transformed trip duration and ARS scale and square-root-
287 transformed foraging range to improve normality and assumed binomial errors for the proportion
288 of U-shaped dives and Poisson errors for dive rate.

289

290 ***Quantifying spatial and environmental consistency***

291 To test hypotheses 1 - 4, we quantified individual consistency in departure directions, coarse to
292 mesoscale (10s km) space use and habitat use. Following Wakefield et al. (Wakefield et al. 2013)
293 we first used movement metrics to identify putative foraging bouts (Appendix C for details).

294 Validation of this approach against known dive locations recorded using TDRs has shown that
295 99% of GPS locations occurring within 10 minutes of known dive locations are classified as
296 foraging. Conversely, 62% of GPS locations classified as foraging occur within 10 minutes of
297 known dives (Wakefield et al. 2013) (note that gannets frequently exhibit search behaviour
298 without diving (35)). We then matched the most spatiotemporally proximate value of each
299 environmental index to each foraging location. In order to describe foraging consistency with
300 respect to relative, rather than absolute environmental covariates, we also considered dynamic
301 covariates standardised by subtracting the mean and dividing by the standard deviation.
302
303 We adopted a simple technique, based on the utilisation distribution (UD), to estimate foraging
304 consistency. UDs quantify not only which locations an animal uses but what proportion of their
305 time they spend in each (Fieberg and Kochanny 2005) and may also be used to describe usage in
306 environmental space. We estimated the foraging UD in Cartesian space ($\hat{UD}_{i,j}(x,y)$) of each
307 individual i , during its j th trip as follows: We first projected foraging locations (longitude and
308 latitude) onto a Lambert equal area projection (x,y) grid. We then estimated their kernel density
309 using the R package ‘adehabitat’ (Calenge 2006), specifying a bivariate normal kernel, a fixed
310 bandwidth (h) of 15 km and a grid resolution of 16 km. We quantified within-individual
311 consistency in the use of space and habitat by calculating the overlap between UDs of multiple
312 trips using Bhattacharyya’s affinity (Fieberg and Kochanny 2005), which ranges from 0 (no
313 similarity between UDs and therefore no spatial consistency) to 1 (identical UDs/perfect spatial
314 consistency). In Cartesian space the overlap between the first and second trips made by the i th
315 bird is:
316

$$\beta_{x,y,i} = \sum_{x,y} \sqrt{\hat{UD}_{i,1}(x,y)\hat{UD}_{i,2}(x,y)} \quad (3)$$

318

319 Similarly, to estimate individual consistency with respect to habitat we estimated β_i in each
 320 dimension k of environmental space (SST, NPP, etc.) by substituting $\hat{UD}_{i,j}(k)$ for $\hat{UD}_{i,j}(x,y)$ in
 321 equation 3. We estimated trip kernel density in the k th dimension of environmental space ($UDk_{i,j}$)
 322 using the R ‘stats’ package (Venables and Ripley 2002). In order to define h for environmental
 323 indices we determined h for each using Scott’s rule (Scott 1992).

324 We quantified individual-level behavioural consistency at two temporal scales: Within-year, we
 325 calculated the mean Bhattacharyya’s affinity $\hat{\beta}_i$ of all pairwise combinations of the first three
 326 trips recorded. Across years, we calculated $\hat{\beta}_i$ of all pairwise combinations of the first trips
 327 recorded in each study year (Fig. 1). We then calculated the population mean consistency $\bar{\beta}$.

328 Hence, $\bar{\beta}$ is based three trips per sampling scale (within or across breeding seasons) making its
 329 magnitude is comparable across scales.

330

331 In itself, $\bar{\beta}$ is not particularly informative because it reflects both population and individual
 332 consistency and cannot therefore be compared directly across usage dimensions. Rather, we used
 333 a randomisation procedure to test the null hypothesis that within-individual consistency in each
 334 dimension is greater than population-level consistency. If the null hypothesis is correct, then
 335 observed consistency should not differ significantly from that when bird identity is randomly
 336 assigned. We estimated the null distribution of $\bar{\beta}$ by randomly reassigning bird identities to trips,
 337 either within or across years, without replacement and recalculating $\bar{\beta}$ and $\bar{\rho}$. To avoid sex-

338 specific behaviour (Stauss et al. 2012) inflating null estimates of this statistic, bird identities were
339 reassigned within sexes. Similarly, trips from different birds made at the same time might be
340 expected, *a priori*, to be more similar than those made at different times. To avoid this
341 potentially inflating our null estimate of $\bar{\beta}$, we reassigned bird identity such that trip order was
342 preserved. For each period, we used 999 permutations. $\bar{\beta}$ cannot be less than the null so we treat
343 this as a one-tailed test.

344

345

346 To test hypotheses 1, 3 and 4 we also quantified individual consistency in departure directions.
347 Variation in the flight direction of gannets relative to the colony diminishes rapidly with colony
348 distance (Pettex et al. 2010). Hence, we defined departure direction as the circular average of the
349 bearing from the colony to the first five locations >10 km from the colony (Patrick et al. 2014).
350 For the *i*th individual, we then estimated directional consistency using mean resultant length $\hat{\rho}_i$
351 of departure directions, which ranges from 0 (no directional consistency) to 1 (all directions
352 equal). We estimated $\hat{\rho}_i$ across three foraging trips. Within years, departure directions were those
353 of the first three trips recorded in that year and across years, those of the first trip recorded in
354 each year (for examples, see Appendix D). We then calculated the population-level mean
355 directional consistency, $\bar{\rho}$ and tested whether this was significantly greater than the null
356 expectation using the randomisation procedure described above. In order to check whether the
357 trip selected affected our conclusions with respect to consistency across years we repeated inter-
358 annual analysis ten times randomly selecting trips birds.

359

360 To test whether directional and spatial consistency within years decayed exponentially over time,
361 we calculated ρ and $\beta_{x,y}$ between pairs of trips separated by different lags, l , where l is the
362 difference in trip number. We then calculated the within-individual mean $\hat{\rho}'_{l,i}$ and $\hat{\beta}'_{x,y,l,i}$ and
363 modelled these indices a function of l , using binomial GLMs and specifying random slopes and
364 intercepts for individuals. We used likelihood ratio tests to determine whether these models
365 explained the data any better than the respective intercept-only models. To test whether
366 directional and spatial consistency declined over successive years, within individuals, we also
367 calculated ρ and $\beta_{x,y}$ between the first trips recorded in 2010 and 2011 and 2010 and 2012.

368

369 *Directedness of trips*

370 The two-dimensional shape of pelagic seabird foraging trips falls on a spectrum between highly
371 linear and highly circuitous (Weimerskirch 2007). To test hypothesis 3, we therefore devised a
372 simple index ρ to quantify the linearity of each trip, which varies between 0 (track describes a
373 circle, with diameter equal to the maximum distance reached from the colony) and 1 (track
374 perfectly linear; Appendix C for further details). For each individual i we calculated $\hat{\kappa}_i$, the
375 mean linearity across trips 1-3 within years and across the first trip recorded in each study year.
376 We then tested the Spearman rank correlation coefficient (r_s) between $\hat{\kappa}$ and indices of foraging
377 repeatability and consistency.

378

379 *Effects of consistency on body condition*

380 In order to quantify between-individual variation in body condition we first tested the
381 dependence of body mass on sex (females are heavier than males (Stauss et al. 2012, Cleasby et
382 al. in press)), culmen length and tarsus length (Votier et al. 2010), using mixed-effects linear

383 models. Most birds were weighed repeatedly across years so individual was specified as a
384 random effect. Assuming this to be the maximal model, we tested the hypotheses that
385 successively simpler models differed from one another using likelihood ratio tests. We assume
386 that residual body mass predicted by the covariates retained varies with body condition. We
387 tested whether this was dependent on individual consistency, repeatability or trip linearity using
388 simple linear models. Not all indices of consistency and repeatability were available for all birds
389 in all years. Hence, to maximise sample sizes, we fitted separate models for each period.

390

391 *Covariance between consistency and repeatability*

392 To determine whether birds that are spatially consistent are also consistent in their use of habitat,
393 we calculated the Spearman rank correlation r_s between spatial and environmental consistency.
394 We used correlation tests to determine whether birds' consistency with respect to space and
395 habitat use covaried with their behavioural or isotopic repeatability. To determine whether birds
396 with narrow diets also forage in a particular manner, we also calculated the correlation between
397 individual isotopic repeatability, behavioural repeatability and consistency with respect to space
398 and habitat. These procedures involved multiple comparisons, so we used the Bonferroni
399 correction to adjust the level of significance to $\pm = 0.05/n$, where n is the number of correlation
400 tests applied in each case. Throughout the rest of the analysis significance was set at $\pm = 0.05$.
401 Unless otherwise stated, medians are quoted with their inter-quartile range (IQR) and means with
402 their 95% confidence intervals.

403

404 **Results**

405 We GPS-logged e 3 consecutive foraging trips from 37, 20 and 31 birds in 2010, 2011 and 2012,
406 respectively, with up to 12 trips per bird in 2010, 14 in 2011 and 7 in 2012. However, some
407 individuals were tracked in only one or two breeding seasons or for <3 trips per season (see
408 Table E1 for details). Birds foraged significantly closer to the colony in 2011 (median distance
409 109, IQR 65 - 175 km) than in 2010 and 2012 (175, 108 - 178 and 160, 97 - 242 km respectively;
410 Fig. 2, Fig. F1, Table E2).

411

412 ***Environmental conditions, variability and fisheries***

413 At the coarse to mesoscale, variation in the physical oceanography of waters accessible to birds
414 from Bass Rock during the study period was relatively low but greater within than across years
415 (Fig. F2, Table E3). The tidal mixing front separating mixed and stratified waters east of
416 Scotland was ~ 30 km closer inshore in 2011 than in 2010 and 2012 (Fig. 1). However, there was
417 little discernible spatial pattern in inter-annual variability in front density or NPP, indicating that
418 these features of the environment were largely predictable at this scale. Mean fishing effort from
419 2007 – 2010 was concentrated: in areas <50 km from the coast to the north and south of Bass
420 Rock, characterised by steep bathymetric relief; over relatively shallow banks (<100 m),
421 offshore, to the east and south east; in the southern Moray Firth, and; in waters north of the 100
422 m isobath, to the northeast of Scotland (Fig. F3).

423

424 ***Diet and isotopic repeatability***

425 Mackerel *Scomber scombrus* were the most abundant species in regurgitates obtained from
426 gannets returning to the colony in all study years, with clupeids (*Sprattus sprattus* and *Clupea*
427 *harengus*) the next most abundant (Table E4). Additionally, sandeels (*Ammodytes spp.*), one

428 garfish *Belone belone* and one langoustine *Nephrops norvegicus*, were recorded in 2011. The
429 median interval between blood-sampling gannets at $t_{y,1}$ and $t_{y,2}$ was 10 days (IQR 9 – 16 days).
430 During all periods blood tissue isotopes varied with tissue type (Table E2). At the inter-annual
431 scale it also varied with year. Baseline environmental isotope levels had little effect on blood
432 tissue isotopes, while sex had significant effects (on $\delta^{13}\text{C}$) only at the inter-annual scale. The
433 isotopic signatures of different prey species recovered from regurgitates were poorly resolved
434 (Fig. F4). However, the adjusted repeatability of $\delta^{15}\text{N}$ in the blood tissues of individuals ($R_{adj} =$
435 0.20 – 0.35) was significant both within and across years, but only marginally so within 2010
436 (Table 1, Table E5). The adjusted repeatability of $\delta^{13}\text{C}$ in blood tissues was significant in 2010
437 and 2011 but not significant in other periods.

438

439 ***Spatial and directional consistency***

440 Gannets tended to depart the colony in directions and forage in areas that were individually
441 consistent, not only within but also across years (Fig. 3, Fig. F5). Mean spatial and directional
442 consistency ($\bar{\beta}_{x,y}$ and $\bar{\rho}$) were significantly greater than the null expectation and were similar
443 within and across years (Fig. 4, Table E6). The method of selecting trips had little effect on our
444 estimates of inter-annual consistency (Table E7). The limited number of gannets that we were
445 able to observe for >3 trips within years exhibited some among-individual variability in spatial
446 consistency. Although the majority of birds remained consistent with time a few individuals were
447 highly inconsistent (Fig. 5). However, within years, we found no significant decay in population
448 mean individual directional or spatial consistency with increasing lag l between trips (Fig. F6,
449 Table E8). Moreover, individual directional consistency between the first trip in years 1 and 2
450 did not differ significantly from that between the first trip in years 1 and 3 (median $\hat{\rho}$, 2010 vs.

451 2011 = 0.99, IQR = 0.98 – 1; 2010 vs. 2012 = 0.99, IQR = 0.98 – 1; paired Wilcoxon signed-
452 rank test $V = 75$, $p = 0.744$, $n = 16$). Similarly, individual spatial consistency did not differ
453 between these periods (median $\hat{\beta}$, 2010 vs. 2011 = 0.32, IQR = 0.24 – 0.44; 2010 vs. 2012 =
454 0.40, IQR = 0.26 – 0.51; paired Wilcoxon signed-rank test $V = 64$, $p = 0.860$, $n = 16$).

455

456 ***Environmental consistency***

457 Individuals foraged at consistent distances from Bass Rock, both within and across years (Fig.
458 4). Individual consistency was highest in 2011 but did not differ from the null expectation,
459 presumably because population level variability in foraging range was low in that year. In all
460 other periods consistency was significant. Gannets foraged both in productive, mixed, inshore
461 waters and less productive, thermally stratified, offshore waters but usage was highest in the
462 former areas, inshore of tidal mixing fronts (cf. Fig. 1, Fig.2 and Fig. F2). Within each study
463 year, individual consistency in habitat use with respect to static and weekly-averaged dynamic
464 environmental indices (range $\bar{\beta}_k = 0.61$ to 0.80) was significantly greater than the null (Fig. 4).
465 In contrast, habitat use was relatively inconsistent across years, except with respect to
466 standardised SST ($\bar{\beta}_{\text{SST}} = 0.74$), which was significantly more consistent than the null. Individual
467 consistency with respect to monthly dynamic environmental indices also followed the pattern
468 described above (Table E6).

469

470 ***Behavioural repeatability***

471 The repeatability of trip durations, the proportion of U-shaped dives and ARS scale was low
472 ($R_{\text{adj}} < 0.07$, Table 1) and not significant, except during 2010, when it was only very marginally
473 so (Table E5). Dive rate was repeatable within 2011 and between 2011 and 2012 but not within

474 2012. Mean dive depth and mean maximum dive depth were significantly repeatable both across
475 years and within years (R_{adj} 0.21 – 0.38, Table 1).

476

477 ***Trip linearity***

478 Most foraging trips were linear rather than circuitous (population median straightness $\bar{\kappa} = 0.85$,
479 IQR 0.80 - 0.89; Fig. 3). However, looping trips were occasionally made (e.g. trip 6, Fig. 5a).

480 Trip linearity did not differ significantly between years (GLMM $z = -1.23$, $p = 0.220$, n birds =
481 55, n trips = 492). Birds that made more linear trips were also more consistent in their departure

482 directions in 2010 (correlation between $\hat{\kappa}$ and $\hat{\rho}$: $r_s = 0.48$, $n = 37$, $p = 0.002$), in the depth of

483 foraging areas in 2011 (correlation between $\hat{\kappa}$ and $\hat{\beta}_{\text{depth}}$: $r_s = 0.60$, $n = 20$, $p = 0.005$) and in the

484 NPP of foraging areas in 2012 (correlation between $\hat{\kappa}$ and $\hat{\beta}_{\text{NPP}}$: $r_s = 0.57$, $n = 26$, $p = 0.003$).

485 Excepting these results, we found no other significant correlations between $\hat{\kappa}$ and indices of
486 consistency or repeatability, nor any consistent patterns within or across years (Table E9).

487

488 ***Covariance in different measures of consistency***

489 Within years, individuals that were spatially more consistent were also more consistent with
490 respect to most static and dynamic environmental covariates (Table E10), except for depth,

491 fishing effort and front density in 2010 and depth in 2011. In contrast, we found no significant

492 correlation between spatial and environmental consistency across years (Table E10). There was

493 little correlation between within-individual behavioural repeatability (R'_{adj}) and foraging

494 consistency with respect to space or the environment ($\hat{\rho}$ and $\hat{\beta}$, Table E11). A notable exception

495 was that in some years individuals with more repeatable trip durations were also more consistent

496 with respect to static environmental indices. In addition, in 2011 (but not 2012) R'_{adj} in either
497 mean or mean maximum dive depth was positively correlated with $\hat{\beta}_{depth}$. Repeatability in ^{13}C in
498 the blood of individuals was not correlated with that of ^{15}N ($r_s = -0.40, 0.07, 0.59$ and -0.17 in
499 2010, 2011 and 2012 and across years respectively; $p > 0.05$ in all cases, $n = 9, 16, 12$ and 22).
500 There were no correlations between blood isotope R'_{adj} and within-individual behavioural
501 repeatability or foraging consistency (Table E12).

502

503 *Effects on body condition*

504 Body mass averaged 2.95 kg (sd = 0.05, $n = 66$). We obtained full morphometric data from 42
505 birds. Within this group, body mass varied significantly with tarsus length, culmen length and
506 sex (marginal $r^2 = 0.43$, Table E13). Females averaged 0.19 kg (95% CI ± 0.09 kg) heavier than
507 males. Residual body mass (RBM) ranged from -0.52 to 0.96 kg (sd = 0.17). Within 2012, RBM
508 was significantly positively related to individual repeatability in trip duration ($F_{1,27} = 6.26$, $r^2 =$
509 0.18 , $p = 0.019$; $RBM = -304.6 + 2752.5 \times R'_{adj}$ trip duration). Other than that, we found no
510 relationship between RBM and indices of consistency, repeatability or track straightness, either
511 within or across years (Table E14).

512

513 **Discussion**

514 Our study shows that northern gannets were individually consistent over three successive
515 breeding seasons in their colony departure directions and coarse to mesoscale (10s km) foraging
516 distribution. To our knowledge this is the first study to test for IFSF across years in seabirds so
517 this phenomenon may be more widespread than hitherto supposed. Indeed, several species of
518 pinniped, which, like seabirds, are wide-ranging marine central-place foragers that target meso-

519 and epipelagic prey, show equivalent long-term behaviours (Bradshaw et al. 2004, Call et al.
520 2008, Baylis et al. 2012). We also found evidence of individual consistency in habitat use with
521 respect to relative SST (rSST) and dietary and behavioural specialisations but these were
522 independent of IFSF. IFSF did not decline over time and was of a similar magnitude within years
523 and across years.

524

525 Mounting loggers on seabirds and handling them repeatedly can raise their temporal and
526 energetic foraging costs (Vandenabeele et al. 2011, Vandenabeele et al. 2012). It is conceivable
527 that this in turn could have led birds in this study to forage in a less exploratory and therefore
528 more repeatable manner than that of the population as a whole. However, in 2010, as part of a
529 parallel study at Bass Rock, we monitored a group of non-instrumented gannets and found that
530 their trip durations were very similar (mean = 23.5 hrs, n = 636 trips from 27 birds, SD = 14.4) to
531 those of the birds we tracked (mean = 23.9 hrs, n = 211 trips from 52 birds, SD = 12.6) (Cleasby
532 et al. in press). Moreover, there is now considerable evidence, collected using a range of
533 technologies to track many species, that IFSF is high within breeding seasons in many seabirds
534 (Weimerskirch 2007, Woo et al. 2008, Patrick et al. 2014). Hence, logger effects are unlikely to
535 have biased our conclusions. Our results, together with evidence that temperate and polar-
536 breeding seabirds forage in relatively predictable environments (Weimerskirch 2007), therefore
537 demand a reappraisal of the view that these seabirds are necessarily highly flexible foragers
538 (Lack 1968). Below we discuss these results in more detail, concentrating on the potential causes
539 and consequences of IFSF in seabirds and other colonial central-place foragers.

540

541 *Does WSLs foraging cause IFSF?*

542 For WSLs foraging (Kamil 1983, Davoren et al. 2003) to be an effective strategy, the rate at
543 which birds switch to new foraging areas should match the temporal scale of environmental
544 variability. Previous studies have assumed implicitly that switches to new foraging areas occur
545 frequently enough to be observable at the scale of days or weeks (Irons 1998). This assumption
546 appears valid in some low latitude breeders which forage in oceanic waters (Weimerskirch 2007,
547 Weimerskirch et al. 2010). However, in temperate, polar and neritic habitats prey patches may be
548 less variable, perhaps persisting across years (Davoren et al. 2003). In accordance with the
549 WSLs hypothesis, we found that spatial consistency in gannets was not absolute (population
550 mean < 0.6 ; Fig. 4) and varied considerably within and among individuals (Fig. 3) due to birds
551 occasionally switching foraging areas, within or between years (Fig. 5b). However, if a WSLs
552 strategy predominated at either temporal scale, IFSF would be expected to decay over time. We
553 found no evidence of this, either over 7 successive foraging trips (i.e. ~ 2 weeks) within breeding
554 seasons or over three successive breeding seasons. Rather, the rate of spatial and directional
555 consistency was similar across years to that within years. Furthermore, though gannets generally
556 travelled directly to foraging areas, birds making more direct trips were no more likely to be
557 consistent with respect to space or environmental indices than those making more circuitous
558 ones. This is difficult to reconcile fully with the hypothesis that gannets anticipate the location of
559 prey prior to departing the colony, switching to more exploratory, circuitous movement patterns
560 only when they encounter poor foraging success (Pettex et al. 2010). Nevertheless, our results do
561 not preclude the possibility that WSLs strategies are matched to longer-term environmental
562 variability. If this were the case, IFSF might break down over periods longer than we observed
563 (~ 2 weeks within years and across 3 years). However, IFSF in pinnipeds and probably some
564 other seabirds persist over decades (Woo et al. 2008, Authier et al. 2012).

565

566 ***Does habitat or dietary specialisation cause IFSF?***

567 Previous studies have shown that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the blood tissues of gannet chicks from Bass
568 Rock (Kakela et al. 2007) and adults breeding in the Celtic Sea (Votier et al. 2010) collected
569 during a single breeding season were repeatable. Given that $\delta^{15}\text{N}$ increases with the trophic
570 position of prey, this may be regarded as evidence of individual dietary specialisation (Bearhop
571 et al. 2006). However, isotopic ratios reflect not only prey type but also the environment from
572 which they come (Moreno et al. 2011), so repeatability of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in individuals' blood
573 tissues could conceivably arise due to individual spatial consistency. The isotopic signatures of
574 prey items we retrieved from breeding gannets poorly resolved individual prey species.
575 Nevertheless, $\delta^{15}\text{N}$ values in the blood tissues of chick-provisioning gannets were significantly
576 repeatable not only within but across years (Table 1), with little or no dependence on baseline
577 ratios (Table E2). Repeatability in $\delta^{13}\text{C}$ was significant within 2011 and 2012 but not across
578 years (Table 1). Blood tissue $\delta^{13}\text{C}$ showed very little dependence on baseline ratios. This is
579 somewhat surprising, given the assumption in seabird isotopic studies that $\delta^{13}\text{C}$ is strongly
580 dependent on the location from which prey are obtained (Cherel and Hobson 2007). However,
581 the shoaling, mesotrophic fish that gannets from the Bass Rock prey upon (sandeels *Ammodytes*
582 spp, mackerel *Scomber scombrus*, herring *Clupea harengus*, etc.; Table E4) are migratory so
583 there may be some mismatch between their isotopic signatures of that of the local environment in
584 which they are captured.

585

586 We sampled blood at an interval of approximately 10 days within each year, so the dietary
587 periods integrated by $\text{RBC}_{y,1}$, $\text{SER}_{y,1}$ and $\text{SER}_{y,2}$ may have overlapped to some extent (Barquete

588 et al. 2013). However, RBC samples collected across years are temporally independent and we
589 controlled for confounding environmental, temporal and intrinsic factors so we are confident that
590 $\delta^{15}\text{N}$ was repeatable at this scale. Our data therefore not only support the supposition that gannets
591 are individual dietary specialists (Kakela et al. 2007, Votier et al. 2010) but also show that
592 specialisations with respect to trophic level persist over multiple breeding seasons.

593

594 Animals with high IFSF also frequently exhibit stereotyped foraging behaviours and habitat
595 preferences (Elliott et al. 2008, Woo et al. 2008, Newsome et al. 2009, Patrick and Weimerskirch
596 2014). However, the relationships between individual consistency in behaviour, diet, habitat use,
597 and space use is complex, and the direction of causality may be unclear (Beverly et al. 2009, Dall
598 et al. 2012). For example, if a prey species are limited to particular locations, IFSF could arise as
599 a consequence of individual dietary specialisations or *vice versa*. We found no evidence of such
600 relationships, indicating that in gannets IFSF and individual dietary specialisation are
601 independent or at most only weakly connected. Alternatively, individual habitat preferences
602 could give rise to IFSF. In our study, individual gannets were consistent with respect to
603 environmental variables within years (see also (Patrick et al. 2014)) and environmental
604 consistency was higher in birds that were more spatially consistent. However, dynamic
605 environmental variables did not differ greatly at the scale of tracking periods within years (i.e. 1
606 – 2 weeks) so this result provides weak evidence for causality. Across years, foraging gannets
607 were also consistent with respect to rSST, which varied markedly (Fig. F2), suggesting that some
608 individuals may track particular stratification regimes, for which rSST is a proxy (Bowers and
609 Simpson 1987). Nevertheless, it is unlikely that individual habitat preferences could account for
610 IFSF because inter-annual IFSF did not correlate with individual consistency with respect to

611 rSST. Moreover, patches of mixed and stratified waters were widely distributed throughout the
612 study area (Fig. F2).

613

614 Within years, gannets with more consistent trip durations were also more consistent with respect
615 to space and static environmental indices. This is most likely because gannet trip durations are
616 proportional to the maximum distance reached from the colony (Hamer et al. 2000). Other links
617 between behavioural repeatability and IFSF were weak or absent. For example, in contrast to a
618 previous study (Patrick et al. 2014), we found very little evidence that dive profiles were
619 repeatable (Table 1; Table E5). Dive rates at Bass Rock within 2011 and across study years, as
620 well as dive depths in all periods, were significantly repeatable. However, there was no
621 relationship between individual repeatability in these behaviours and consistency with respect to
622 spatial, environmental or isotopic consistency. Moreover, the scale of ARS did not differ
623 significantly between individuals. ARS scale may therefore be dependent on factors common to
624 all individuals, such as the scale of prey patches, which is limited by physical processes
625 (Fauchald and Tveraa 2006).

626

627 *Does site familiarity cause IFSF?*

628 Given the weak evidence to support the hypothesis that IFSF is driven predominantly by other
629 forms of individual consistency or a short-term WSLs strategy, we consider another hypothesis:
630 that foraging site fidelity in gannets results, in part at least, from site familiarity (Irons 1998,
631 Piper 2011). Until recently the role of site familiarity in habitat selection was largely overlooked
632 in favour of the ideal free/ideal despotic models, which make the unrealistic assumption that
633 animals are perfectly informed about their environment (Fretwell and Lucas 1969) or models that

634 emphasise the role of information gain from public sources (Ward and Zahavi 1973, Danchin et
635 al. 2001). However, recent habitat selection studies suggest that it may be more advantageous for
636 animals to remain in familiar locations than hitherto supposed (Piper 2011). Indeed, the
637 investment made in site familiarity can explain decisions to remain at relatively poor quality sites
638 (the ‘always stay strategy’ (Switzer 1993)). During breeding, when energetic demands are high
639 and time constraints severe, foraging in a familiar location may be less risky than exploring more
640 widely (this leads to the testable prediction that IFSF will be higher in breeding birds than in less
641 constrained birds, such as failed breeders). Moreover, remaining in a familiar location may
642 advantage individuals by reducing competition from less well informed conspecifics (Piper
643 2011). By analogy with other forms of individual specialisation, this implies that IFSF may be a
644 density-dependent phenomenon (Araujo et al. 2011).

645

646 Prior to first breeding, immature seabirds prospect at multiple colonies, potentially using public
647 information to assess site quality (Danchin et al. 2001, Votier et al. 2011). This life history stage
648 lasts longer in pelagic seabirds than in most other avian groups, an adaption thought to allow
649 individuals to learn to forage effectively in the marine environment (Lack 1968), but the
650 considerable investment made in the breeding site during this time may also account for the high
651 degree of philopatry in seabirds. Furthermore, the tendency for foraging site familiarity to accrue
652 with age may act to canalise foraging site decisions, to the extent that adult IFSF is high. This
653 process of experience-mediated behavioural canalisation is similar a mechanism hypothesised to
654 explain the phenomenon of wintering site fidelity (*ortstreue*), which is widespread in migratory
655 birds (Alerstam 1990, Guilford et al. 2011).

656

657 ***The roles of environmental predictability and behavioural flexibility***

658 A potential cost of IFSF and specialisation is that individuals lack the flexibility to respond to
659 environmental change (Bolnick et al. 2003). Early theories of seabird life history traits and
660 behaviour were founded on the assumption that seabirds forage in such stochastic environments
661 (Lack 1968). For example, the information centre hypothesis posits that seabirds use public
662 information, acquired at the colony, to locate ephemeral prey patches (Ward and Zahavi 1973).
663 Only one study has provided direct support for the information centre hypothesis in seabirds
664 (Weimerskirch et al. 2010) and evidence of short-term IFSF has been regarded as contrary to this
665 hypothesis (Irons 1998). However, indirect evidence suggests that foraging *Morus* spp. exploit
666 both private and public information (Wakefield et al. 2013). At the population-level, gannets
667 from Bass Rock are clearly flexible, both in diet (Table E4, (Hamer et al. 2007)) and range (Fig.
668 2 and Fig. F1). During our study, individual dietary specialisation and spatial, environmental and
669 behavioural consistency, while significant, were not absolute (Fig. 4). Rather, birds sometimes
670 switched between foraging areas (Fig. 3 and Fig. 5b). A possible explanation is that foraging
671 strategies differ with life history stage, site familiarity and environmental conditions (Piper
672 2011). Exploratory behaviour, aided by public information, is likely only during immaturity or
673 when foraging success is low (Ward and Zahavi 1973), while the benefits of IFSF are likely to
674 increase with age (Pärt 1995). However, adults may retain flexibility by using a hierarchical
675 strategy. It is notable that some of our study birds were consistent in their departure directions
676 but less so in their foraging areas (Fig. 3). Gannets may therefore be faithful primarily to a
677 directional arc, rather than an area *per se* (Hamer et al. 2001). By departing the colony within
678 this arc they would remain in familiar waters yet have scope to travel further from the colony if
679 foraging success is poor during the early stages of a trip (the ‘trap line’ strategy (Wanless et al.

680 1990)). Only if foraging success was poor throughout the favoured arc would they then switch to
681 another, guided either by memory or the movements of conspecifics from the colony.
682
683 The optimal strategy will also depend on environmental predictability (Switzer 1993). For
684 example, IFSF in lactating New Zealand fur seals (*Arctocephalus forsteri*) is higher in neritic
685 than oceanic waters, which is thought to reflect the degree of predictability in these two habitats
686 (Baylis et al. 2012). Temperate and polar seabirds forage on much more predictable resources
687 than hitherto supposed (Weimerskirch 2007) and there is now abundant evidence that, far from
688 being featureless and stochastic, neritic waters are highly structured by predictable factors, such
689 as bathymetry and the tides (Fig. F2) (Bowers and Simpson 1987, Scott et al. 2010). Our study
690 shows that, at the coarse scale, foraging gannets target individually consistent locations,
691 suggesting that at this scale the occurrence of prey is predictable. At finer scales gannets use
692 ARS and local enhancement to locate their prey (Hamer et al. 2009), implying that the
693 predictability of prey is considerably lower at these scales. This accords with the hierarchical
694 patch model of seabird prey (Fauchald and Tveraa 2006). As such, it is likely that IFSF is scale
695 dependent and declines rapidly below the coarse scale. Foraging ranges during our study were
696 low to intermediate when compared to those recorded at Bass Rock in previous years (Fig. F1).
697 Given that foraging range increases in years of low prey availability (Hamer et al. 2007, Garthe
698 et al. 2011), this suggests that prey were in good supply during our study. Furthermore, we found
699 that environmental variability in the area exploited by Bass Rock gannets was lower across years
700 than that within years during our study (Table E3, Fig. F2), suggesting that the location of prey
701 may have been predictable across years. In years of lower food availability or predictability IFSF
702 may be less marked than we observed.

703
704 Given our evidence of individual IFSF and specialisation with respect to diet, habitat (relative
705 SST) and behaviour (dive rate and mean dive depth) in gannets, it is pertinent to ask whether
706 these traits confer fitness advantages. We found only weak evidence that that residual body mass
707 was dependent upon consistency of foraging behaviour. However, the fitness consequences of
708 IFSF in black-browed albatrosses *Thalassarche melanophris* and southern elephant seals
709 *Mirounga leonina* are only apparent over decadal time scales (Authier et al. 2012, Patrick and
710 Weimerskirch 2014). Ultimately, longer-term tracking, combined with dietary, environmental
711 and demographic monitoring, will be required to determine the persistence, proximate causes and
712 fitness consequences of IFSF in breeding seabirds.

713

714 ***Wider implications***

715 Our study, together with others on pinnipeds, bats and ants, suggests that IFSF may be a trait
716 common to colonial central-place foragers. Increasingly, tracking studies are conducted to
717 estimate the distributions of wide-ranging marine species, such as seabirds and pinnipeds, for
718 conservation purposes. If IFSF is widespread in this group, the implication is that research
719 resources would be better directed to tracking many individuals for short representative periods
720 in the life history stages of interest, rather than fewer individuals for longer. However, resource
721 selection models fitted to such data generally make the implicit assumptions that foragers are
722 perfectly informed about their environment and select the most favourable habitats (Fretwell and
723 Lucas 1969) but the effects of site familiarity and fidelity, as well as dietary and habitat
724 specialisation are rarely considered (Piper 2011, Dall et al. 2012). As a consequence, such
725 models may over-predict the degree to which animals track spatiotemporally patchy resources.

726 Indeed, long-term strategies that give rise to IFSF may account for the observation that at shorter
727 time scales there is frequently a mismatch between the coarse-scale distribution of seabirds and
728 their prey (Grémillet et al. 2008, Fauchald et al. 2011). It is frequently suggested that seabirds
729 and other higher predators, such as pinnipeds, can be used to monitor the state of the marine
730 environment (Boyd et al. 2006), yet the tendency for IFSF and dietary specialisation to weaken
731 the link between predator demography and short-term environmental variability implies that this
732 may be less fruitful than otherwise supposed. Importantly, if IFSF does arise through site
733 familiarity, this implies that environmental conditions experienced during development may
734 have lifetime consequences (Dall et al. 2012). Moreover, rapid climate change may have an
735 unexpected cost on seabirds if their life history strategy is reliant on the veracity of site-specific
736 information gained early in their long lives (Hipfner 2008). Given this and the many other
737 potential implications of IFSF and specialisation in colonial central-place foragers (Bradshaw et
738 al. 2004, Weimerskirch 2007, Call et al. 2008) we urge that long term longitudinal tracking
739 studies be employed to test for these phenomena and alternative explanatory hypotheses in other
740 members of this group.

741

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748

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959

960

961 **Supplemental Material**

962

963 **Appendix A.**

964 Sources and pre-processing of environmental data used in the analysis.

965

966 **Appendix B.**

967 Additional description of the methods used to determine gannet tissue and environmental

968 baseline stable isotope ratios.

969

970 **Appendix C.**

971 Additional description of methods used to quantify and classify the behaviour of gannets at sea.

972

973 **Appendix D.**

974 Illustration of individual foraging consistency indices using contrasting examples.

975

976 **Appendix E.**

977 Additional results tables, including details on sample sizes; foraging models; environmental
978 variability; diet; individual repeatability and consistency; correlations among behavioural and
979 dietary indices; morphology and its dependence on behavioural and isotopic repeatability.

980

981 **Appendix F.**

982 Additional results figures, including inter-annual variation in foraging range; dynamic
983 environmental conditions during the study; static environmental covariates considered; prey and
984 gannet blood stable isotope ratios; all tracks of gannets foraging from Bass Rock; and directional
985 and spatial consistency across successive trips within years.

986

987 **Table 1.** Repeatability (R_{adj}) of foraging behaviour and blood stable isotope ratios in chick-
 988 provisioning gannets[†].

Statistic	R_{adj}			
	Within 2010	Within 2011	Within 2012	Across years
$\delta^{15}\text{N}$	0.20	0.35	0.35	0.33
$\delta^{13}\text{C}$	0.37	0.55	0.18	0.03
Trip duration	0.04	0.02	0.01	0.01
ARS scale	0.01	0.01	0.02	0.02
Dive rate	-	0.50	0.04	0.43
Proportion U-shaped dives	-	0.07	0.00	0.00
Mean dive depth	-	0.38	0.37	0.36
Mean max dive depth	-	0.37	0.29	0.21

989 Values in **bold** are significant based on 95% credible intervals (Table E5).

990 [†] For sample sizes see Table E2.

991

992

993 **Figure legends**

994

995 **Fig. 1.** Study area, showing (a) depth (25 m contours), Bass Rock (yellow triangle) and other
996 locations mentioned in the text: 1. Moray Firth; 2. NE Scotland coastal waters; 3. Farnes Deep,
997 4. Dogger Bank. (b) Average summertime SST, 2010 – 2012. The 13 °C isotherms in July 2010,
998 2011 and 2012 (blue, red and black lines respectively) indicate the approximate interface
999 between mixed and stratified waters in those years. Dashed lines show 100 km intervals of
1000 distance-by-sea from Bass Rock.

1001

1002 **Fig. 2.** Foraging distribution of chick-provisioning northern gannets tracked from Bass Rock
1003 during June-August, 2010, 2011 and 2012. UD = mean foraging Utilisation Distribution
1004 estimated using the first 3 trips recorded from each individual tracked for e 3 trips in each year
1005 (37, 20 and 31 birds respectively). Smoothing parameter $h = 15$ km. Dashed lines indicate 100
1006 km intervals of distance-by-sea from Bass Rock (yellow triangle).

1007

1008 **Fig. 3.** The first track of chick-rearing gannets recorded in each year (red = 2010; blue = 2011;
1009 green = 2012). Panels corresponding to each bird (identity bottom right) are arranged in
1010 descending order of spatial consistency across years ($\bar{\beta}^i_{x,y}$). Birds illustrated were tracked for e
1011 1 trip in each study year (for the full dataset see Fig. F5). Dashed lines show 100 km intervals
1012 from Bass Rock. $\bar{\rho}$ = directional consistency across years.

1013

1014 **Fig. 4.** Mean consistency of gannets over three foraging trips (coloured symbols) compared to
1015 the null distribution expectation (5th, 25th, 75th and 95th percentiles) determined by randomly

1016 reassigning bird identity to tracks 999 times without replacement (see Table E6 for details).
1017 Colours and symbols indicate the probability that mean consistency is significantly greater than
1018 the null. x, y = Cartesian space; SST = sea surface temperature; FD = front density; NPP = net
1019 primary production. Dynamic environmental covariates were averaged by week prior to analysis.

1020

1021 **Fig. 5.** Most gannets were consistent in their colony departure directions and foraging locations
1022 (e.g. **a**). However, a minority were largely inconsistent (e.g. **b**). Numbers indicate terminal
1023 locations of successive trips in 2010 (colours grade from red to blue with time). Yellow triangle
1024 = Bass Rock.

1025