

1 **Frequency and consequences of individual dietary specialisation in a wide-**
2 **ranging marine predator, the Northern Gannet**

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16 **Running Head:** Consequences of dietary specialisations under intraspecific
17 competition

18

19 **Abstract**

20 Individual specialisations in animals are important contributors to a wide range of
21 ecological and evolutionary processes, and have been particularly documented in
22 relation to multiple aspects of foraging behaviours. Central-place foragers, such as
23 seabirds, frequently exhibit pronounced specialisations and individual differences in a

24 variety of foraging traits. In particular, the availability of fisheries discards alongside
25 natural prey resources provides additional potential for differentiation and
26 specialisation for opportunistically scavenging seabird species. However, the
27 consequences of such specialisations for at-sea distributions and intra-specific
28 interactions are not well known. Here we investigate the links between the degree of
29 dietary specialisation on natural or discard prey and the foraging movements and
30 spatial occupancy of Northern Gannets *Morus bassanus*, in relation to differing
31 intraspecific competition at six differently sized colonies. We found that, at most
32 colonies, individuals with different dietary strategies concentrated foraging at
33 differing levels of intraspecific competition. In addition, individuals pursuing
34 different strategies were frequently, but not consistently, spatially separated,
35 distinctions that were most acutely seen in females. However, this variation in
36 individual strategy had no significant impact on current body condition. These
37 analyses demonstrate how foraging-associated metrics need not covary within an
38 unconstrained system. They also reveal that specialisation can have important
39 consequences for the competitive regimes individuals experience, highlighting the
40 complexity of examining interacting consequences at large spatial scales.

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43 **Keywords:** fisheries, foraging, GPS, individual specialisation, stable isotope analysis,
44 seabird

45

46 **Introduction**

47 Individual variation among animals is increasingly identified across a broad range of
48 traits, and is key to understanding a range of ecological, evolutionary and applied
49 issues (Van Valen 1965, Araújo et al 2011, Wennersten & Forsman 2012). While
50 examining variation at broader levels of classification, for example sex or age classes,
51 can reveal relevant distinctions, significant variation is often left unexplained by such
52 analyses, particularly in population-level generalists (Bearhop et al 2004, Araujo et al
53 2011). Individual-level investigation can then be informative in explaining additional
54 variation as, in many cases, organism responses, and their extent of specialisation
55 across a range of attributes, differ among individuals (Bolnick et al 2003, Araujo et al
56 2011). Indeed, such variation among individuals frequently exceeds that within any
57 one individual and, by spanning time or contexts, can result in long-term consistencies
58 or behavioural syndromes (Dall et al 2012, Sih et al 2012).

59 Such specialisations have been shown to be theoretically and experimentally produced
60 by increasing levels of competition (Svanback & Bolnick 2005, 2007, Bolnick et al
61 2010), with inter-individual differences significant in reducing levels of competition
62 among conspecifics (Dit Durell 2000, Svanback & Bolnick 2007, Araujo et al 2011,
63 Tinker et al 2012, Machovsky-Capuska et al 2016a). Here, competitive interactions
64 can affect individual prey choice preferences, producing differentiation between
65 individuals within a single locality, and increasing the overall population niche width
66 (Svanback & Bolnick 2007, Araujo et al 2011, Ingram et al 2011). These results
67 typically rely on identifying whole food items, but there is also the potential for
68 individuals to further specialise from a nutritional perspective through the selection of
69 nutritionally complementary prey (Tait et al 2014, Machovsky-Capuska et al 2016a,
70 2016b). Regardless of the level of selectivity, persistent differences in prey

71 consumption among individuals can then lead to the establishment of dietary
72 specialisations (Sih et al 2012). Divergence in strategies can also occur through the
73 movement of individuals displaced from areas of high competitive pressure. Such
74 movements may lead to the discovery of different prey fields or foraging
75 environments, with specialisations establishing among individuals in terms of their
76 response to environmental cues and area occupancy across space or time (Bodey et al
77 2014, Patrick et al 2014, Wakefield et al 2015). Thus, there are potential adaptive
78 advantages to specialisation in many situations (Bolnick et al 2011, Dall et al 2012,
79 Machovsky-Capuska et al 2016b), but the links between competitive and
80 environmental influences, and how these shape the consequences of specialisation,
81 remain poorly understood.

82 Colonially breeding marine vertebrates (e.g. seabirds and pinnipeds) are excellent test
83 subjects for hypotheses about the consequences of individual specialisations,
84 particularly with respect to foraging behaviours such as travel and prey searching
85 (Ceia & Ramos 2015). The constraints of colonial breeding produce intraspecific
86 competition for prey among colony members (Lewis et al 2001, Villegas-Amtmann et
87 al 2013), and the presence of neighbouring colonies can also constrain foraging
88 opportunities (Wakefield et al 2013, 2017). Such conditions can favour individual
89 tactics that reduce competition with conspecifics, and this may be more keenly seen at
90 larger colonies where higher densities of individuals can produce stronger competitive
91 effects (Tinker et al 2012, Ceia & Ramos 2015, Kernaléguen et al 2015). The
92 consequences of specialisation in such central-place foragers may thus be seen either
93 through sympatric differentiation in measures including colony niche width (Araujo et
94 al 2011, Bolnick et al 2011), or through changes in spatial distribution. These
95 differences in occupancy can be generated through both deliberate choice and

96 competitive exclusion. For example, juvenile red knots *Calidris canutus* are forced to
97 forage for longer, and in more dangerous localities, through direct competitive
98 interference by adults (van den Hout et al 2014). Alternatively, different foraging
99 specialisations, including maintaining a generalist strategy, can represent equally
100 successful approaches for avoiding interference in what are, amongst marine
101 predators, often scramble competition situations (Woo et al 2008, Machovsky-
102 Capuska et al 2016a). Importantly, the extent to which an individual pursues any
103 specialist or generalist strategy can have a broad range of consequences. This is
104 clearly seen in the exploitation of new foraging opportunities such as fisheries
105 discards. Despite being novel from an evolutionary perspective, a number of seabird
106 species now routinely exploit such anthropogenic resources (Oro et al 1996,
107 Bartumeus et al 2010, Wagner & Boersma 2011, Bicknell et al 2013, Bodey et al
108 2014, Patrick et al 2015, Pirotta et al 2018), and specialisation on discards can
109 dramatically affect an individual's long-term fitness, either directly through changes
110 in adult body condition or mortality, or indirectly through effects on timing of
111 reproduction or chick survival (Grémillet et al 2008, Bicknell et al 2013).

112 Here we examine the consequences of specialism in foraging strategies at multiple
113 colonies of the Northern Gannet *Morus bassanus* (hereafter gannet). We combine
114 information from GPS loggers with stable isotope analysis (SIA) of blood samples
115 from individuals from six colonies spanning more than one order of magnitude in size
116 (~2 000 to ~60 000 pairs) in differing oceanographic environments. We hypothesise
117 that: (i) different dietary specialisations, in terms of specific prey species consumed,
118 will explain variation in foraging movement metrics because different prey are likely
119 to be associated with different environmental cues (Scales et al 2014, Cleasby et al
120 2015a, Wakefield et al 2015), and (ii) individuals pursuing different foraging

121 strategies will be more divergent in space use at larger colonies as a result of the
122 increased competitive pressures present (Lewis et al 2001, Wakefield et al 2013). We
123 also explore the consequences of different foraging strategies for seasonal measures
124 of individual fitness (body condition and breeding performance). Anthropogenic
125 resources have been suggested to be nutritionally inferior to naturally foraged prey
126 (Annett & Pierotti 1999, Gremillet et al 2008, Votier et al 2010, Tait et al 2014,
127 Machovsky-Capuska et al 2016a). We therefore hypothesise that (iii) individuals that
128 incorporate high proportions of discards (anthropogenic resources) in their diets will
129 have poorer body condition than those that specialise on naturally available prey.

130

131

132 **Material and methods**

133 **Field Data Collection**

134 Gannets were captured, and then recaptured for device removal (i.e. a total of two
135 captures per individual), at six island colonies over 38 days from late Jun to early Aug
136 2011, ensuring overlapping of tracking and sampling at all colonies (table 1). Chick-
137 rearing adults (chicks \geq 2 weeks post-hatching, identified from Nelson 2001, range 2-
138 7 weeks) were caught at the nest during parental changeover using a brass noose or
139 crook on the end of a carbon fibre pole. 30 g passive GPS loggers ('i-gotu' GT200e,
140 MobileAction Technology) or 45 g GPS Radio Frequency loggers (e-obs GmbH,
141 Germany) were deployed depending on colony accessibility. All devices were
142 attached to the base of the central tail feathers using Tesa© tape, as used in previous
143 studies at many of these colonies (Votier et al 2010, Cleasby et al 2015a), and
144 acquired locations every 2 minutes. Birds with passive loggers were recaptured using
145 the same methodology approximately 12 days later (mean time over which trips were
146 recorded 11.5 days, range 4 – 15); table 1) for device removal. A small blood sample
147 (0.2 – 1.0 ml) was taken from the tarsal vein at both capture and recapture from most
148 individuals for sexing and SIA. Blood samples were kept in a cooler (1-7hr) until
149 undergoing centrifugation to separate red blood cells (RBC) from plasma. Separated
150 samples were then kept at -20°C until being dried and homogenised for analysis. Diet
151 samples were also collected from all colonies through opportunistic collection of
152 spontaneous regurgitates from both handled birds and other breeding individuals
153 disturbed during the capture process. These were necessarily limited in number by our
154 focus on capturing departing adults i.e. those that had already fed and brooded their
155 chick, often for many hours, and typically had empty stomachs, and our ethical
156 decision to not unduly disturb other birds at each colony. Prey items were identified to

157 the lowest possible taxon and then stored at -20°C until undergoing lipid extraction
158 prior to isotopic analysis (see ESM).

159 **Determination of Dietary Specialisations**

160 Dietary specialisations were identified using Bayesian stable isotope mixing models
161 fitted in the SIAR package (Parnell et al 2010) to assign proportions of different prey
162 species in the diets of individuals. This involved analysing the isotopic ratios of $\delta^{15}\text{N}$
163 and $\delta^{13}\text{C}$ for RBC from initial capture of individuals to determine the proportions of
164 different food sources consumed, reflecting diet over approximately the previous
165 month (Hobson & Clark 1992). Data from 149 individuals, comprising birds where
166 GPS devices were both successfully and unsuccessfully retrieved, were included, with
167 lipid extracted prey samples from the specific colony of the individual in question
168 used as sources because colony foraging areas are largely discrete (Wakefield et al
169 2013). Using these estimates of dietary components, individuals were then classified
170 as specialists if they met two *a priori* criteria: i) the modal prey item estimate for an
171 individual must be greater than one standard deviation above the average of all birds
172 sampled at that colony; and ii) the prey item in question must comprise >30% of the
173 individual's total diet. These criteria together accounted for both variation in resource
174 availability across colonies, and dietary importance in a species with a broad foraging
175 capability (Nelson 2001, Hamer et al 2007), although they do not consider variation in
176 the nutritional composition of prey that may add additional subtlety (Machovsky-
177 Capuska et al 2016b). Specialists were further categorised as either forage fish
178 specialists (e.g. consumers of mackerel *Scomber scombrus*) or those that specialised
179 on demersal discards (whitefish, see ESM). Individuals with diets that did not meet
180 these criteria were classed as generalists.

181

182 **GPS Data Processing and Movement Metrics**

183 Only complete foraging trips were included in analyses of foraging behaviour. In
184 addition, all locations within 1 km of the colony were deleted as individuals only use
185 these areas for bathing and rafting (Carter et al 2016). Three metrics assessing
186 different components of foraging behaviour were calculated from each individual trip:
187 a) total trip length (km), reflecting effort expended; b) angle of departure (the average
188 over the first five bearings > 1 km from the colony, degrees), reflecting the extent to
189 which an individual uses past knowledge, and; c) maximum distance from the colony
190 (km), combining energy expended with both personal and public information use. In
191 addition, for each GPS location L_0 , speed (between L_{-1} and L_0) and tortuosity (the
192 degree to which the tracked animal's path diverges from a straight line between L_{-4}
193 and L_0) were determined. Putative foraging locations were then identified based on
194 these parameters as described in Wakefield et al (2013). Colony-specific utilization
195 distributions (UDs) were then estimated to enable investigation of the levels of intra-
196 specific competition likely to be experienced by gannets foraging in different
197 locations (see Habitat Selection below). The colony mean kernel density (KD) for all
198 putative foraging locations was calculated based on a 2 km Lambert Azimuthal Equal
199 Area grid using the R package `adehabitatHR` (Calenge 2007). Individuals were
200 tracked for different lengths of time, so the KD was estimated for each individual with
201 the smoothing parameter h estimated by least-squares cross-validation. The mean
202 smoothing parameter, \bar{h} was then used to estimate the KD for each individual, and
203 this was averaged across individuals within colonies. UD were then calculated for
204 the 95, 75, 50 and 25% levels at each colony.

205 **Consequences of Foraging Strategies**

206 *Links between Dietary Specialisations and Movement Metrics*

207 We used three generalised linear mixed models (GLMMs), one for each movement
208 metric, to examine whether the identified foraging strategies significantly influenced
209 foraging metrics. These models included sex and colony as fixed effects known to
210 influence foraging behaviours (Stauss et al 2012, Cleasby et al 2015a) as well as the
211 random effect of individual. We examined whether there was an additional effect of
212 dietary specialisation (n = 88 individuals spanning all colonies with full data
213 required). Models were compared using an information theoretical approach, with the
214 model with the lowest AICc score regarded as the top model. However, in instances
215 where the top model included an extra term that did not improve the model AICc
216 score by more than two units, the most parsimonious model is also highlighted, as
217 such additional terms can be regarded as uninformative (Arnold 2010). Goodness of
218 fit was assessed using the likelihood-ratio based pseudo-R-squared (Nakagawa &
219 Schielzeth 2013).

220 *Habitat Selection*

221 We used Habitat Selection Functions (HSFs) to model the foraging range usage by birds
222 within each of the three dietary categories as a function of the level of competition
223 experienced. HSFs compare spatial locations that are used versus unused but available,
224 adopting a logistic-regression based approach with a case-control design (Aarts et al
225 2008). This generates a binomial response that takes the value 1 for the *i*th data point if
226 it belongs to the dataset of putative foraging locations or the value 0 if it belongs to the
227 control dataset. The control dataset consisted of five pseudo-absences selected

228 randomly within the 95% UD of each colony matched to each observed foraging
229 location.

230 To estimate the level of competition experienced by gannets when foraging we
231 calculated the density of individuals at each point as $\hat{u}_{i,x}N_i$ where $\hat{u}_{i,x}$ is the estimated
232 absolute density of use of cell x (cell size = 4 km²) by birds from colony i , and N_i is the
233 number of breeding pairs at the i th colony (Wakefield et al 2013). This approach
234 incorporates information on colony size and allows for adjustment for how bird density
235 declines within a colony's foraging range with increasing distance from the colony, and
236 UDs thus calculated match data from at-sea surveys (Cleasby et al 2015b). In addition,
237 while we were not able to include data on prey availability as fish distributions are not
238 measured synoptically over the scale with which we tracked gannets, individuals from
239 several of these study colonies are known to repeatedly cue in on stable oceanographic
240 features (Scales et al 2014, Cleasby et al 2015a). As the foraging ranges of some
241 colonies partially overlapped, we summed the spatial density estimates across grid
242 squares at these locations (Figure S1). While small untracked colonies from which
243 overlaps cannot be calculated are located within the study area, these colonies represent
244 <5% of the total birds foraging across the entire area, so additional competitive
245 interactions will be minimal.

246 HSFs were estimated using a binomial generalised additive mixed model (GAMM) in
247 the mgcv R package (Wood 2006). The response variable was whether a location was
248 used (1) or not (0), with the level of competition at each location included as a smoother.
249 In our full model we estimated separate competition smoothers for each foraging
250 specialisation category by colony combination (e.g. 'Bass Rock - Forage Fish' or
251 'Grassholm - Generalist'). Bird identity nested within colony identity was included as
252 random intercepts, and a thin-plate regression spline for the spatial coordinates of each

253 data point was included to account for spatial auto-correlation (ESM). From this initial
254 model, minimum adequate models were selected by backwards selection using K -fold
255 cross-validation ($K = 5$; ESM), using the summed log-likelihood values for the holdout
256 data as a goodness-of-fit measure.

257 ***Body Condition***

258 Body condition was measured in the field as a seasonal fitness proxy as offspring
259 recruitment rates and lifetime individual breeding success are not known in this
260 system. This was estimated using the scaled mass conditional index (Peig & Green
261 2009). Body mass was measured (± 50 g) on initial capture when the stomach was
262 empty, and scaled to the mean maximum tarsus length (see ESM). This index was
263 calculated using data from 176 individuals across all colonies. It is hypothesised that a
264 higher scaled mass is an indicator of individuals with higher fitness because breeding
265 is a demanding process which is likely to reduce body condition. The effect of
266 specialisation on scaled mass was assessed using a general linear model (GLM) with a
267 Gaussian error structure, and the full model included all two-way interactions between
268 colony, sex and dietary type. Simplified models were compared using AICc scores,
269 with consideration of both the top ranked and the most parsimonious models. Normal
270 q-q plots confirmed that all model residuals conformed to assumptions of normality
271 and all analyses were conducted in R v3.4.3 (R Core Team 2017).

272 **Results**

273 112 individuals were successfully tracked across the six colonies (mean per colony:
274 19 ± 8), producing 810 complete foraging tracks (range per individual: 2 – 20, table
275 1). 149 individuals were blood sampled (mean per colony: 25 ± 11 , including 98
276 successfully tracked individuals). The great majority of individuals were categorised
277 as generalists, with the proportion of specialists of either kind varying substantially
278 between colonies (table 1).

279 *Links between Dietary Specialisations and Movement Metrics*

280 The top models for all movement metrics contained the effects of sex and colony,
281 confirming the known increase in foraging distances at larger colonies (Lewis et al
282 2001), and reflecting the fact that females typically travel greater distances than males
283 (Cleasby et al 2015a; figure 1, table 2). Dietary specialisation had an important effect
284 only on the maximum distance birds moved from their colony (figure 1, table 2, table
285 S1). Females tended to travel further than males in all categories, but this was most
286 pronounced in forage fish specialists. Conversely, female discard specialists travelled
287 substantially smaller maximum distances from the colony than other females. Males
288 changed little in maximum displacement distance regardless of dietary type.

289 **Consequences of Foraging Strategies**

290 *Habitat Selection*

291 Based on K-fold cross-validation, the best predictive HSF was one that incorporated
292 separate competition smoothers for each foraging specialisation category on a colony-
293 by-colony basis (tables S2, S3). This indicates that the relationship between foraging
294 specialisation and the density of conspecifics encountered at sea varied both among

295 strategies and colonies, despite the fact that, within a colony, similar total ranges of
296 competition were experienced (figure 2). This result was also reflected spatially, with
297 individuals pursuing different foraging strategies often diverging in geographical
298 locations visited (figure 2).

299 At the two largest colonies at which discard use was recorded (Ailsa Craig and
300 Grassholm, figure 2), discard specialists showed greater usage of foraging areas with
301 higher levels of competition, with usage rapidly reducing in areas of lower competitive
302 pressure. In contrast, forage fish specialists showed a reversal of this trend. While
303 central-place foraging necessarily means they experience the highest levels of
304 competition, peak predicted usage rose above that of other dietary types at lower levels
305 of competition, indicating that forage fish specialists spent more foraging effort in areas
306 with low conspecific densities. Generalist foragers showed a similar pattern to discard
307 specialists, but with a weaker selective response to areas of high competition. Similar
308 results were also observed at the largest colony (Bass Rock, figure 2) where generalist
309 foragers were predicted to make greater use of areas with higher conspecific
310 competition than forage fish specialists, with usage reversed at the lowest levels of
311 competition (no discard regurgitates were identified here in 2011). However, such
312 differentiation between strategies was not apparent on the west coast of Ireland, where
313 colonies showed little spatial differentiation and strategies followed similar trajectories
314 across the competition gradient. Lastly, at the smallest colony (Great Saltee, figure 2)
315 neither specialist type extensively foraged under the higher levels of competition
316 experienced by generalists.

317 *Body Condition*

318 Females were significantly heavier than males at most colonies, but dietary type had
319 no impact on scaled mass (figure S2, S3, table 3).

320

321 **Discussion**

322 Our results demonstrate how, in an unconstrained system across multiple populations
323 and environmental conditions at large spatial scales, variation in dietary strategy can
324 have consequences for spatial separation in, and the competitive environments
325 experienced by, an apex predator. We demonstrate that individuals specialising on
326 forage fish showed greater usage of areas of reduced competitive pressure (i.e. lower
327 densities of conspecifics) compared to either discard specialists or generalists (figure
328 2). However, dietary specialisations were also present in some instances without
329 broad spatial separation in foraging locations, highlighting the degree to which
330 environmental variation is important in facilitating the realisation of specialisations.
331 We also show that there is significant variation in foraging movements between
332 females, but not males, pursuing different strategies (figure 1). However, these
333 individual differences had limited consequences for our measured fitness correlate
334 (body condition), suggesting that different strategies may represent alternative
335 successful solutions to cope with interspecific competitive effects in this species.

336 When considering links between dietary specialisations and foraging movements we
337 only found support for differences in maximum displacement from the colony.
338 Females tended to travel farther than males within all strategies (figure 1) and, within
339 females, forage fish specialists reached significantly more distant points than discard
340 specialists. This movement metric reflects a degree of both the effort involved and the
341 use of both public and private knowledge, and suggests that individuals pursuing all
342 strategies have favoured search localities or environmental triggers that they will
343 repeatedly target (Dall et al 2012, Masello et al 2013, Patrick et al 2014, Wakefield et
344 al 2015). However, we found no significant relationships between the pursuit of
345 different dietary strategies and either trip length or departure angle. This in turn

346 suggests that diverse localities and patch types were available within all colonies'
347 foraging ranges, and that, for individuals pursuing all strategies, time to locate food
348 patches varied between trips in this dynamic environment (Scales et al 2014,
349 Wakefield et al 2015). This lack of commonality between the extent of specialisation
350 in prey selection and in multiple foraging movements suggests that these two
351 components may not form a behavioural syndrome in this species (Sih et al 2012).
352 Behaviours may simply be linked across time periods (Wakefield et al 2015); or
353 certain foraging techniques and locations may be best suited to certain individual
354 phenotypes (Lewis et al 2002, Dall et al 2012).

355 However, we did find that birds exhibiting different dietary strategies (generalists,
356 forage fish or discard specialists) frequently experienced different competitive
357 regimes while foraging (figure 2), and while sample sizes at any one colony could be
358 relatively small, this pattern was repeated at several of our study colonies. This
359 suggests that an interaction between foraging preference and the degree of
360 competition experienced at a location may well affect the foraging decisions of
361 individuals and thus explain repeatable displacement distances from the colony
362 (Corman et al 2016). Forage fish specialists, particularly females, tended to fly further
363 (figures 1, 2), and Bartumeus et al (2010) demonstrated that such foraging on natural
364 prey tends to create a superdiffusive movement process characterised by longer
365 flights. This suggests an alternative strategy that may be employed by females in
366 particular as a result of competitive exclusion by more aggressive males at discarding
367 opportunities (Nelson 2001, Lewis et al 2002, Stauss et al 2012). Alternatively, it may
368 reflect certainty of parentage and a willingness to 'work harder' at chick provisioning
369 (Kokko & Jennions 2008), or differences in nutritional demands, particularly post-egg
370 production, between the sexes (Machovsky-Capuska et al 2016a, Botha & Pistorius

371 2018). Contrastingly, we found that discard specialists travel shorter distances and
372 experience higher competition, supporting a subdiffusive movement pattern for
373 discard specialists (Bartumeus et al 2010, figure 2). Becoming a discard specialist has
374 been suggested to provide large volumes of food with reduced flying (and therefore
375 energetic) costs for adults, although with additional costs in terms of nutritional
376 quality (Grémillet et al 2008, van Donk et al 2017). However, remaining closer to the
377 colony will naturally lead to individuals foraging in areas where greater numbers of
378 conspecifics are present. Our results suggest that any energetic benefits of exploiting
379 discards through reduced commuting costs, may be offset by greater conspecific
380 competitive pressures and the potential for conflicts this can produce at a spatially
381 concentrated resource. This potential cost-benefit scenario for the exploitation of
382 discards should be explored further with respect to its potential to affect population
383 growth at individual colonies.

384 Interestingly, while most apparent at larger colonies, clearer spatial separation of
385 different strategies was not consistently achieved with increasingly colony size,
386 although such spatial divergence between different strategies has been demonstrated
387 theoretically and on smaller mesocosm scales (Svanback & Bolnick 2005, 2007,
388 Bolnick et al 2010). For example, dietary specialisation was achieved by some
389 individuals at the most western colonies (Bull Rock and Little Skellig) despite almost
390 complete overlap in foraging space and competitive environments experienced (figure
391 2), and a substantial difference in these colony sizes. Breeding gannets are almost
392 exclusively foragers in neritic waters (Nelson 2001), and the closer proximity of the
393 shelf break to these colonies compresses both natural and anthropogenic foraging
394 opportunities into a smaller area, such that variation in ecological opportunities may
395 be maintained despite spatial restrictions. Contrastingly, at the smallest colony (Great

396 Saltee), there was clear spatial separation between forage fish specialists and discard
397 specialists, likely reflecting the high levels of discards available in the southern Irish
398 Sea (Anonymous 2011). These results highlight alternative ways in which ecological
399 opportunities can facilitate the maintenance of dietary specialisations, and emphasise
400 the necessity of considering the interactions between intraspecific competition and
401 ecological opportunity in order to understand when and how individuals are able to
402 achieve foraging differentiation (Roughgarden 1974, Parent & Crespi 2009, Araujo et
403 al 2011).

404 Although proportions were neither consistent across colonies, or scaled with colony
405 size, we found far more individuals followed generalist than specialist strategies
406 amongst those sampled. While gannets are capable of taking a wider range of prey
407 than many other sympatric seabirds (Nelson 2001), and thus may seem to have a
408 greater potential for developing individual specialisations, their foraging opportunities
409 are often constrained by conspecific interference competition (Garthe & Huppopp
410 1998, Lewis et al 2001, Votier et al 2013). When combined with inter-annual changes
411 in prey availability and environmental parameters (Hamer et al 2007), this may
412 preclude high degrees of specialisation and ensure individuals are able to respond to
413 changeable conditions (Hamer et al 2007, Dall et al 2012) while meeting their
414 nutritional requirements (Machovsky-Capuska et al 2016a). This potential for
415 flexibility may also explain why, despite variation in habitat usage and distances
416 covered in response to competitive and environmental pressures, different foraging
417 strategies did not affect adult scaled mass. Although specialisation on forage fish and
418 discards has previously been linked to better and poorer body condition respectively
419 at one of these colonies (Grassholm, Votier et al 2010), a similar result was not found
420 when examining the relationship across multiple colonies (with the exception of Great

421 Saltee, figure S3). However, as outlined above, this relationship may vary across
422 years as a consequence of changes in prey field availability and nutritional
423 composition (Hamer et al 2001, Scales et al 2014, Tait et al 2014, Wakefield et al
424 2015, Machovsky-Capuska et al 2016a), and may also be affected by sample sizes.
425 The only other clear distinction was that, at the largest colonies, the scaled mass of
426 individuals tended to be lower. This could be due to competition-driven increases in
427 foraging range impacting on body condition (Lewis et al 2001), or it may be a
428 strategic decision to reduce wing loading to facilitate longer flights. Whether this has
429 any important effects on longevity or reproductive output remains unknown,
430 particularly as differences may become apparent only under particularly unfavourable
431 conditions or when individuals are followed over many years (Annett & Pierotti 1999,
432 Hamer et al 2007, Lescroel et al 2010). This is especially likely as long-lived adults
433 maintain a wide safety margin in body mass, prioritising self-maintenance over
434 current provisioning, potentially requiring much longer-term individual based studies
435 to determine fitness effects (Lecomte et al 2010).

436 Our findings demonstrate that dietary specialisations can have important
437 consequences for the competitive regimes that individual gannets experience and, at
438 several colonies, although sample sizes were relatively small, this can result in spatial
439 separation of individuals of specialist and generalist foraging strategies. This pattern
440 was seen at both small and large colonies that were located away from shelf breaks,
441 suggesting that intraspecific competitive effects are not the sole contributor to these
442 patterns. For example, interspecific effects may mirror intraspecific interactions at
443 multi-species aggregations leading to disruption of feeding opportunities, with such
444 interspecific competitive regimes often important in affecting species foraging
445 distributions (Balance et al 1997, Ronconi & Burger 2011, Dhondt 2012). The

446 interactions between foraging specialisations and competition are nuanced, and the
447 consequences found here highlight the complexity of examining interacting
448 consequences at large spatial scales.

449

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456 blood sampling were all conducted under appropriate regional licenses. This study
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462 **Data Accessibility**

463 Tracking data are available from Birdlife International at
464 http://seabirdtracking.org/mapper/contributor.php?contributor_id1/4207. Data for the
465 models presented in Table 2 is included as an additional supplementary file to the
466 manuscript.

467

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658 Table 1: Fieldwork locations, sample sizes and foraging strategy categorisations. Colony sizes are apparently occupied nests (AON) counted in
 659 2004 except for ^a surveyed in 2009 (<http://jncc.defra.gov.uk/smp/>). Retrieved devices are those from which data were successfully recovered.

Colony name	Geographical location	Colony size (AON)	Devices retrieved with multiple complete trips & deployment dates	Median number of trips/individual	Individuals sampled for SIA		Generalists	Forage fish specialists	Discard specialists
					Male	Female			
Great Saltee, Ireland	52° 06' N 06° 37' W	2 400	18 2 – 19 Jul	9	13	20	26 (79%)	4 (12%)	3 (9%)
Bull Rock, Ireland	51° 35' N 10° 18' W	3 700	14 28 Jun – 15 Jul	12.5	16	11	15 (56%)	6 (22%)	6 (22%)
Ailsa Craig, Scotland, UK	55° 15' N 05° 06' W	27 100	16 7 – 22 Jul	7	5	11	11 (69%)	2 (13%)	3 (19%)
Little Skellig, Ireland	51° 46' N 10° 30' W	29 700	9 11 – 23 Jul	7	5	5	6 (60%)	3 (30%)	1 (10%)
Grassholm, Wales, UK	51° 43' N 05° 28' W	39 300 ^a	30 25 Jun – 29 Jul	7	22	18	22 (55%)	8 (20 %)	10 (25%)

Bass Rock, Scotland, UK	56° 05' N 02° 24' W	55 500	25 26 Jun – 2 Aug	6	14	9	19 (82%)	4 (18%)	0 (0%)
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661

662 Table 2. Comparison of mixed models examining the effect of dietary specialization
 663 on foraging movement metrics. The top model determined by AIC ranking for each
 664 metric is presented in bold, and the most parsimonious model in italics (see Methods
 665 for more details). The variance explained by the top model for each metric (and the
 666 most parsimonious where relevant) is also presented.

Model	Δ AIC compared to top model for each foraging metric		
	Trip distance (km)	Maximum distance from colony (km)	Departure angle (°)
Sex + Colony	0.00	5.17	24.00
Sex + Dietary Type	33.62	38.73	72.08
Colony + Dietary Type	4.61	7.01	16.39
Sex + Colony + Dietary Type	0.86	5.21	15.28
Sex + Colony + Sex*Colony	1.56	3.31	<i>0.36</i>
Sex + Colony + Dietary Type + Sex*Dietary Type	0.38	<i>0.72</i>	17.00
Sex + Colony + Dietary Type + Sex*Colony	2.25	4.39	0.00
Sex + Colony + Dietary Type + Sex*Colony + Sex*Dietary Type	1.70	0.00	3.65
Null	35.89	39.10	86.84
Goodness of fit top	0.199	0.295	0.475
Goodness of fit <i>most parsimonious</i>	-	0.284	0.471

667

668

669 Table 3. Comparison of general linear models examining the effect of dietary
670 specialization on scaled mass of adult gannets. The top model determined by AIC
671 ranking is presented in bold, and the most parsimonious model in italics (see Methods
672 for more details). The variance explained by the top model is also presented.

673

Model	Δ AIC compared to top model
	Scaled mass
Colony + Sex	<i>0.00</i>
Colony + Sex + Colony*Sex	4.14
Colony + Sex + Dietary Type	2.72
Colony + Sex + Dietary Type + Colony*Sex	6.64
Colony + Sex + Dietary Type + Sex*Dietary Type	4.04
Sex	5.49
Dietary Type	11.17
Sex + Dietary Type	7.18
Colony	5.85
Null	10.15
Goodness of fit for top model	0.143

674

675

676 Figure 1. Maximum distance travelled from the colony on foraging trips (averaged
677 across all colonies) depends on gannet dietary type and sex (females = dark bars,
678 males = white bars, boxes represent interquartile range and median). Number of
679 individuals within each dietary type (generalist: F=24, M=30; forage fish specialist:
680 F=12, M=3; discard specialist: F=6, M=12).

681

682

683 Figure 2. Habitat selection function (HSF) and utilisation distribution (UD) plots for
684 different dietary types (generalists = black; forage fish specialists = red; discard
685 specialists = blue) at each of the study colonies. Lefthand panels: HSF plots show
686 how usage changes with the level of competition at each colony. Solid lines indicate
687 the smoother from the fitted model, reflecting the predicted strength of choice of those
688 competitive conditions for the different foraging strategies, with dashed lines showing
689 95% confidence intervals. Note the x-axis for competition has been reversed so that
690 the highest levels of competition (closer to the colony) appear to the left. Righthand
691 panels: Maps showing the 50% (solid line) and 95% (dashed line) UD of different
692 dietary