Frequency and consequences of individual dietary specialisation in a wide-ranging marine predator, the northern gannet

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ABSTRACT: Individual specialisations in animals are important contributors to a wide range of ecological and evolutionary processes, and have been particularly documented in relation to multiple aspects of foraging behaviours. Central-place foragers, such as seabirds, frequently exhibit pronounced specialisations and individual differences in a variety of foraging traits. In particular, the availability of fisheries discards alongside natural prey resources provides additional potential for differentiation and specialisation for

29 opportunistically scavenging seabird species. However, the consequences of such

30 specialisations for at-sea distributions and intraspecific interactions are not well known. Here,

31 we investigated the links between the degree of dietary specialisation on natural or discarded

32 prey and the foraging movements and spatial occupancy of northern gannets Morus bassanus

33 in relation to differing intraspecific competition at 6 colonies of differing sizes. We found

34 that, at most colonies, individuals with different dietary strategies concentrated foraging at

35 differing levels of intraspecific competition. In addition, individuals pursuing different

36 strategies were frequently, but not consistently, spatially separated, distinctions that were

37 most acutely seen in females. However, this variation in individual strategy had no significant

38 impact on current body condition. These analyses demonstrate how foraging-associated

39 metrics need not covary within an unconstrained system. They also reveal that specialisation

40 can have important consequences for the competitive regimes individuals experience,

41 highlighting the complexity of examining interacting consequences at large spatial scales.

42 KEY WORDS: Fisheries · Foraging · GPS · Individual specialisation · Stable isotope

43 analysis · Seabird

INTRODUCTION

45   Individual variation among animals is increasingly identified across a broad range of

46 traits, and is key to understanding a range of ecological, evolutionary and applied issues (Van

47 Valen 1965, Araújo et al. 2011, Wennersten & Forsman 2012). While examining variation at

48 broader levels of classification, for example sex or age classes, can reveal relevant

49 distinctions, significant variation is often left unexplained by such analyses, particularly in

50 population-level generalists (Bearhop et al. 2004, Araújo et al. 2011). Individual-level

51 investigation can then be informative in explaining additional variation as, in many cases,

52 organism responses, and their extent of specialisation across a range of attributes, differ

53 among individuals (Bolnick et al. 2003, Araújo et al. 2011). Indeed, such variation among

54 individuals frequently exceeds that within any one individual and, by spanning time or

55 contexts, can result in long-term consistencies or behavioural syndromes (Dall et al. 2012,

56 Sih et al. 2012).

57   Such specialisations have been shown to be theoretically and experimentally

58 produced by increasing levels of competition (Svanbäck & Bolnick 2005, 2007, Bolnick et al.

59 2010), with inter-individual differences significant in reducing levels of competition among

60 conspecifics (Durell 2000, Svanbäck & Bolnick 2007, Araújo et al. 2011, Tinker et al. 2012,

Machovsky-Capuska et al. 2016a). Here, competitive interactions can affect individual prey choice preferences, producing differentiation between individuals within a single locality, and increasing the overall population niche width (Svanbäck & Bolnick 2007, Araújo et al. 2011, Ingram et al. 2011). These results typically rely on identifying whole food items, but there is also the potential for individuals to further specialise from a nutritional perspective through the selection of nutritionally complementary prey (Tait et al. 2014, Machovsky-Capuska et al. 2016a,b). Regardless of the level of selectivity, persistent differences in prey consumption among individuals can then lead to the establishment of dietary specialisations (Sih et al. 2012). Divergence in strategies can also occur through the movement of individuals displaced from areas of high competitive pressure. Such movements may lead to the discovery of different prey fields or foraging environments, with specialisations establishing among individuals in terms of their response to environmental cues and area occupancy across space or time (Bodey et al. 2014, Patrick et al. 2014, Wakefield et al. 2015). Thus, there are potential adaptive advantages to specialisation in many situations (Bolnick et al. 2011, Dall et al. 2012, Machovsky-Capuska et al. 2016b), but the links between competitive and environmental influences, and how these shape the consequences of specialisation, remain poorly understood.

Colonially breeding marine vertebrates (e.g. seabirds and pinnipeds) are excellent test subjects for hypotheses about the consequences of individual specialisations, particularly with respect to foraging behaviours such as travel and prey searching (Ceia & Ramos 2015). The constraints of colonial breeding produce intraspecific competition for prey among colony members (Lewis et al. 2001, Villegas-Amtmann et al. 2013), and the presence of neighbouring colonies can also constrain foraging opportunities (Wakefield et al. 2013, 2017). Such conditions can favour individual tactics that reduce competition with conspecifics, and this may be more keenly seen in larger colonies where higher densities of individuals can produce stronger competitive effects (Tinker et al. 2012, Ceia & Ramos 2015, Kernaléguen et al. 2015). The consequences of specialisation in such central-place foragers may thus be seen either through sympatric differentiation in measures including colony niche width (Araújo et al. 2011, Bolnick et al. 2011), or through changes in spatial distribution. These differences in occupancy can be generated through both deliberate choice and competitive exclusion. For example, juvenile red knots Calidris canutus are forced to forage for longer durations, and in more dangerous localities, through direct competitive interference by adults (van den Hout et al. 2014). Alternatively, different foraging specialisations,

including maintaining a generalist strategy, can represent equally successful approaches for avoiding interference in what are, amongst marine predators, often scramble competition situations (Woo et al. 2008, Machovsky-Capuska et al. 2016a). Importantly, the extent to which an individual pursues any specialist or generalist strategy can have a broad range of consequences. This is clearly seen in the exploitation of new foraging opportunities such as fisheries discards. Despite being novel from an evolutionary perspective, a number of seabird species now routinely exploit such anthropogenic resources (Oro et al. 1996, Bartumeus et al. 2010, Wagner & Boersma 2011, Bicknell et al. 2013, Bodey et al. 2014, Patrick et al. 2015, Pirotta et al. 2018), and specialisation on discards can dramatically affect an individual's long-term fitness, either directly through changes in adult body condition or mortality, or indirectly through effects on timing of reproduction or chick survival (Grémillet et al. 2008, Bicknell et al. 2013).

Here, we examined the consequences of specialism in foraging strategies at multiple colonies of the northern gannet Morus bassanus (hereafter gannet). We combined information from GPS loggers with stable isotope analysis (SIA) of blood samples from individuals from 6 colonies spanning more than one order of magnitude in size (~2000 to **~60 000** pairs) in differing oceanographic environments. We hypothesised that (1) different dietary specialisations, in terms of specific prey species consumed, will explain variation in foraging movement metrics because different prey are likely to be associated with different environmental cues (Scales et al. 2014, Cleasby et al. 2015a, Wakefield et al. 2015), and (2) individuals pursuing different foraging strategies will be more divergent in space use at larger colonies as a result of the increased competitive pressures present (Lewis et al. 2001, Wakefield et al. 2013). We also explored the consequences of different foraging strategies for seasonal measures of individual fitness (body condition and breeding performance). Anthropogenic resources have been suggested to be nutritionally inferior to naturally foraged prey (Annett & Pierotti 1999, Grémillet et al. 2008, Votier et al. 2010, Tait et al. 2014, Machovsky-Capuska et al. 2016a). We therefore hypothesised that (3) individuals that incorporate high proportions of discards (anthropogenic resources) in their diets will have poorer body condition than those that specialise on naturally available prey.

MATERIALS AND METHODS

Field data collection

Gannets were captured, and then recaptured for device removal (i.e. a total of 2 captures ind.$^{-1}$), at 6 island colonies over 38 d from late June to early August 2011, ensuring overlapping of tracking and sampling at all colonies (see Table 1). Chick-rearing adults (chicks ≥2 wk post-hatching [range 2–7 wk], identified from Nelson 2001) were caught at the nest during parental changeover using a brass noose or crook on the end of a carbon fibre pole. Passive GPS loggers (30 g; i-gotu GT200e; MobileAction Technology) or GPS radio frequency loggers (45 g; e-obs) were deployed, depending on colony accessibility. All devices were attached to the base of the central tail feathers using Tesa$^{©}$ tape, as used in previous studies at many of these colonies (Votier et al. 2010, Cleasby et al. 2015a), and acquired locations every 2 min. Birds with passive loggers were recaptured using the same methodology approximately 12 d later (mean time over which trips were recorded: 11.5 d, range 4–15 d; see Table 1) for device removal. A small blood sample (0.2–1.0 ml) was taken from the tarsal vein from most individuals during both capture and recapture, for sexing and SIA. Blood samples were kept in a cooler (1–7 h) until undergoing centrifugation to separate red blood cells (RBC) from plasma. Separated samples were then kept at –20°C until being dried and homogenised for analysis. Diet samples were also collected from all colonies through opportunistic collection of spontaneous regurgitates from both handled birds and other breeding individuals disturbed during the capture process. These were necessarily limited in number by our focus on capturing departing adults, i.e. those that had already fed and brooded their chick, often for many hours, and typically had empty stomachs, and by our ethical decision to not unduly disturb other birds at each colony. Prey items were identified to the lowest possible taxon and then stored at –20°C until undergoing lipid extraction prior to isotopic analysis (see ESM).

Determination of dietary specialisations

Dietary specialisations were identified using Bayesian stable isotope mixing models fitted in the SIAR package (Parnell et al. 2010) to assign proportions of different prey species in the diets of individuals. This involved analysing the isotopic ratios of $\delta^{15}N$ and $\delta^{13}C$ for RBC from initial capture of individuals to determine the proportions of different food sources consumed, reflecting diet over approximately the previous month (Hobson & Clark 1992). Data from 149 individuals, comprising birds where GPS devices were both successfully and unsuccessfully retrieved, were included, with lipid-extracted prey samples from the specific colony of the individual in question used as sources because colony foraging areas are largely

157 discrete (Wakefield et al. 2013). Using these estimates of dietary components, individuals

158 were then classified as specialists if they met 2 a priori criteria: (1) the modal prey item

159 estimate for an individual must be >1 SD above the average of all birds sampled at that

160 colony; and (2) the prey item in question must comprise >30% of the individual's total diet.

161 These criteria together accounted for both variation in resource availability across colonies,

162 and dietary importance in a species with a broad foraging capability (Nelson 2001, Hamer et

163 al. 2007), although they do not consider variation in the nutritional composition of prey that

164 may add additional subtlety (Machovsky-Capuska et al. 2016b). Specialists were further

165 categorised as either forage fish specialists (e.g. consumers of mackerel Scomber scombrus)

166 or those that specialised on demersal discards (whitefish; see ESM). Individuals with diets

167 that did not meet these criteria were classed as generalists.

GPS data processing and movement metrics

169   Only complete foraging trips were included in analyses of foraging behaviour. In

170 addition, all locations within 1 km of the colony were deleted as individuals only use these

171 areas for bathing and rafting (Carter et al. 2016). Three metrics assessing different

172 components of foraging behaviour were calculated from each individual trip: (1) total trip

173 length (km), reflecting effort expended; (2) angle of departure (the average over the first 5

174 bearings >1 km from the colony, degrees), reflecting the extent to which an individual uses

175 past knowledge; and (3) maximum distance from the colony (km), combining energy

176 expended with both personal and public information use. In addition, for each GPS location

177 L_0, speed (between L_{-1} and L_0) and tortuosity (the degree to which the tracked animal's path

178 diverges from a straight line between L_{-4} and L_0) were determined. Putative foraging

179 locations were then identified based on these parameters as described in Wakefield et al.

180 (2013). Colony-specific utilisation distributions (UDs) were then estimated to enable

181 investigation of the levels of intraspecific competition likely to be experienced by gannets

182 foraging in different locations (see 'Habitat selection' below). The colony mean kernel

183 density (KD) for all putative foraging locations was calculated based on a 2 km Lambert

184 azimuthal equal-area grid using the R package 'adehabitatHR' (Calenge 2007). Individuals

185 were tracked for different lengths of time, so the KD was estimated for each individual with

186 the smoothing parameter h estimated by least-squares cross-validation. The mean smoothing

187 parameter, $\bar{h}$ was then used to estimate the KD for each individual, and this was averaged

across individuals within colonies. UDs were then calculated for the 95, 75, 50 and 25% levels at each colony.

Consequences of foraging strategies

Links between dietary specialisations and movement metrics

We used 3 generalised linear mixed models (GLMMs), one for each movement metric, to examine whether the identified foraging strategies significantly influenced foraging metrics. These models included sex and colony as fixed effects known to influence foraging behaviours (Stauss et al. 2012, Cleasby et al. 2015a) as well as the random effect of individual. We examined whether there was an additional effect of dietary specialisation (n = 88 ind. spanning all colonies with full data required). Models were compared using an information theoretical approach, with the model with the lowest Akaike's information criterion for small samples (AIC_c) score regarded as the top model. However, in instances where the top model included an extra term that did not improve the model AIC_c score by more than 2 units, the most parsimonious model was also highlighted, as such additional terms can be regarded as uninformative (Arnold 2010). Goodness-of-fit was assessed using the likelihood-ratio based pseudo-R^2 (Nakagawa & Schielzeth 2013).

Habitat selection

We used habitat selection functions (HSFs) to model the foraging range usage by birds within each of the 3 dietary categories as a function of the level of competition experienced. HSFs compare spatial locations that are used vs. unused-but-available, adopting a logistic regression based approach with a case-control design (Aarts et al. 2008). This generates a binomial response that takes the value 1 for the ith data point if it belongs to the data set of putative foraging locations, or the value 0 if it belongs to the control data set. The control data set consisted of 5 pseudo-absences selected randomly within the 95% UD of each colony matched to each observed foraging location.

To estimate the level of competition experienced by gannets when foraging, we calculated the density of individuals at each point as as $\hat{u}_{i,x}N_i$, where $\hat{u}_{i,x}$ is the estimated absolute density of use of cell x (cell size = 4 km^2) by birds from colony i, and N_i is the number of breeding pairs at the ith colony (Wakefield et al. 2013). This approach incorporates information on colony size and allows for adjustment for how bird density declines within a

218 colony's foraging range with increasing distance from the colony, and UDs thus calculated

219 match data from at-sea surveys (Cleasby et al. 2015b). In addition, while we were not able to

220 include data on prey availability, as fish distributions are not measured synoptically over the

221 scale with which we tracked gannets, individuals from several of these study colonies are

222 known to repeatedly cue in on stable oceanographic features (Scales et al. 2014, Cleasby et

223 al. 2015a). As the foraging ranges of some colonies partially overlapped, we summed the

224 spatial density estimates across grid squares at these locations (see Fig. S1 in Supplement 1 at

225 www.int-res.com/articles/suppl/mXXXpXXX_supp.pdf). While small untracked colonies

226 from which overlaps could not be calculated were located within the study area, these

227 colonies represent <5% of the total birds foraging across the entire area, so additional

228 competitive interactions will be minimal.

229 HSFs were estimated using a binomial generalised additive mixed model (GAMM) in

230 the R package 'mgcv' (Wood 2006). The response variable was whether a location was used

231 (1) or not (0), with the level of competition at each location included as a smoother. In our

232 full model, we estimated separate competition smoothers for each foraging specialisation

233 category by colony combination (e.g. 'bass rock – forage fish' or 'grassholm – generalist').

234 Bird identity nested within colony identity were included as random intercepts, and a thin-

235 plate regression spline for the spatial coordinates of each data point was included to account

236 for spatial auto-correlation (ESM). From this initial model, minimum adequate models were

237 selected by backwards selection using K-fold cross-validation (K = 5; ESM), using the

238 summed log-likelihood values for the holdout data as a goodness-of-fit measure.

Body condition

240 Body condition was measured in the field as a seasonal fitness proxy, as offspring

241 recruitment rates and lifetime individual breeding success are not known in this system. This

242 was estimated using the scaled mass conditional index (Peig & Green 2009). Body mass was

243 measured (±50 g) on initial capture when the stomach was empty, and scaled to the mean

244 maximum tarsus length (see ESM). This index was calculated using data from 176

245 individuals across all colonies. It is hypothesised that a higher scaled mass is an indicator of

246 individuals with higher fitness because breeding is a demanding process which is likely to

247 reduce body condition. The effect of specialisation on scaled mass was assessed using a

248 general linear model (GLM) with a Gaussian error structure, and the full model included all

249 2-way interactions between colony, sex and dietary type. Simplified models were compared

using AIC_c scores, with consideration of both the top ranked and the most parsimonious models. Normal Q-Q plots confirmed that all model residuals conformed to assumptions of normality, and all analyses were conducted in R v.3.4.3 (R Core Team 2017).

RESULTS

A total of 112 individuals were successfully tracked across the 6 colonies (mean ± SD per colony: 19 ± 8), producing 810 complete foraging tracks (range per ind.: 2–20; Table 1). Blood samples were taken from 149 individuals (mean per colony: 25 ± 11, including 98 successfully tracked individuals). The majority of individuals were categorised as generalists, with the proportion of specialists of either kind varying substantially between colonies (Table 1).

Links between dietary specialisations and movement metrics

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

Consequences of foraging strategies

Habitat selection

Based on K-fold cross-validation, the best predictive HSF was one that incorporated separate competition smoothers for each foraging specialisation category on a colony-by-colony basis (Tables S2 & S3 in Supplement 1). This indicates that the relationship between foraging specialisation and the density of conspecifics encountered at sea varied both among strategies and colonies, despite the fact that, within a colony, similar total ranges of competition were experienced (Fig. 2). This result was also reflected spatially, with individuals pursuing different foraging strategies often diverging in geographical locations visited (Fig. 2).

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

Body condition

Females were significantly heavier than males at most colonies, but dietary type had no impact on scaled mass (Figs. S2 & S3, Table 3).

DISCUSSION

Our results demonstrate how, in an unconstrained system across multiple populations and environmental conditions at large spatial scales, variation in dietary strategy can have consequences for spatial separation in, and the competitive environments experienced by, an apex predator. We demonstrated that individuals specialising on forage fish showed greater usage of areas of reduced competitive pressure (i.e. lower densities of conspecifics) compared to either discard specialists or generalists (Fig. 2). However, dietary specialisations were also present in some instances without broad spatial separation in foraging locations, highlighting the degree to which environmental variation is important in facilitating the realisation of specialisations. We also showed that there is significant variation in foraging movements between females, but not males, pursuing different strategies (Fig. 1). However,

311   these individual differences had limited consequences for our measured fitness correlate

312   (body condition), suggesting that different strategies may represent alternative successful

313   solutions to cope with interspecific competitive effects in this species.

314   When considering links between dietary specialisations and foraging movements, we

315   only found support for differences in maximum displacement from the colony. Females

316   tended to travel farther than males within all strategies (Fig. 1) and, within females, forage

317   fish specialists reached significantly more distant points than discard specialists. This

318   movement metric reflects a degree of both the effort involved and the use of both public and

319   private knowledge, and suggests that individuals pursuing all strategies have favoured search

320   localities or environmental triggers that they will repeatedly target (Dall et al. 2012, Masello

321   et al. 2013, Patrick et al. 2014, Wakefield et al. 2015). However, we found no significant

322   relationships between the pursuit of different dietary strategies and either trip length or

323   departure angle. This in turn suggests that diverse localities and patch types were available

324   within all colonies' foraging ranges, and that, for individuals pursuing all strategies, time to

325   locate food patches varied between trips in this dynamic environment (Scales et al. 2014,

326   Wakefield et al. 2015). This lack of commonality between the extent of specialisation in prey

327   selection and in multiple foraging movements suggests that these 2 components may not form

328   a behavioural syndrome in this species (Sih et al. 2012). Behaviours may simply be linked

329   across time periods (Wakefield et al. 2015), or certain foraging techniques and locations may

330   be best suited to certain individual phenotypes (Lewis et al. 2002, Dall et al. 2012).

331   However, we did find that birds exhibiting different dietary strategies (generalists,

332   forage fish or discard specialists) frequently experienced different competitive regimes while

333   foraging (Fig. 2), and while sample sizes at any one colony could be relatively small, this

334   pattern was repeated at several of our study colonies. This suggests that an interaction

335   between foraging preference and the degree of competition experienced at a location may

336   well affect the foraging decisions of individuals and thus explain repeatable displacement

337   distances from the colony (Corman et al. 2016). Forage fish specialists, particularly females,

338   tended to fly further (Figs. 1 & 2), and Bartumeus et al. (2010) demonstrated that such

339   foraging on natural prey tends to create a super-diffusive movement process characterised by

340   longer flights. This suggests an alternative strategy that may be employed by females in

341   particular as a result of competitive exclusion by more aggressive males at discarding

342   opportunities (Nelson 2001, Lewis et al. 2002, Stauss et al. 2012). Alternatively, it may

343   reflect certainty of parentage and a willingness to 'work harder' at chick provisioning (Kokko

344 & Jennions 2008), or differences in nutritional demands, particularly post-egg production,

345 between the sexes (Machovsky-Capuska et al. 2016a, Botha & Pistorius 2018). Contrastingly,

346 we found that discard specialists traveled shorter distances and experienced higher

347 competition, supporting a sub-diffusive movement pattern for discard specialists (Bartumeus

348 et al. 2010) (Fig. 2). Becoming a discard specialist has been suggested to provide large

349 volumes of food with reduced flying (and therefore energetic) costs for adults, although with

350 additional costs in terms of nutritional quality (Grémillet et al. 2008, van Donk et al. 2017).

351 However, remaining closer to the colony will naturally lead to individuals foraging in areas

352 where greater numbers of conspecifics are present. Our results suggest that any energetic

353 benefits of exploiting discards through reduced commuting costs may be offset by greater

354 conspecific competitive pressures and the potential for conflicts this can produce at a

355 spatially concentrated resource. This potential cost–benefit scenario for the exploitation of

356 discards should be explored further with respect to its potential to affect population growth at

357 individual colonies.

358   Interestingly, while most apparent at larger colonies, clearer spatial separation of

359 different strategies was not consistently achieved with increasing colony size, although such

360 spatial divergence between different strategies has been demonstrated theoretically and on

361 smaller mesocosm scales (Svanbäck & Bolnick 2005, 2007, Bolnick et al. 2010). For

362 example, dietary specialisation was achieved by some individuals at the most western

363 colonies (Bull Rock and Little Skellig) despite almost complete overlap in foraging space and

364 competitive environments experienced (Fig. 2), and a substantial difference in these colony

365 sizes. Breeding gannets are almost exclusively foragers in neritic waters (Nelson 2001), and

366 the closer proximity of the shelf break to these colonies compresses both natural and

367 anthropogenic foraging opportunities into a smaller area, such that variation in ecological

368 opportunities may be maintained despite spatial restrictions. Contrastingly, at the smallest

369 colony (Great Saltee), there was clear spatial separation between forage fish specialists and

370 discard specialists, likely reflecting the high levels of discards available in the southern Irish

371 Sea (Anonymous 2011). These results highlight alternative ways in which ecological

372 opportunities can facilitate the maintenance of dietary specialisations, and emphasise the

373 necessity of considering the interactions between intraspecific competition and ecological

374 opportunity in order to understand when and how individuals are able to achieve foraging

375 differentiation (Roughgarden 1974, Parent & Crespi 2009, Araújo et al. 2011).

Although proportions were neither consistent across colonies, nor scaled with colony size, we found far more individuals followed generalist than specialist strategies amongst those sampled. While gannets are capable of taking a wider range of prey than many other sympatric seabirds (Nelson 2001), and thus may seem to have a greater potential for developing individual specialisations, their foraging opportunities are often constrained by conspecific interference competition (Garthe & Huppop 1998, Lewis et al. 2001, Votier et al. 2013). When combined with inter-annual changes in prey availability and environmental parameters (Hamer et al. 2007), this may preclude high degrees of specialisation and ensure individuals are able to respond to changeable conditions (Hamer et al. 2007, Dall et al. 2012) while meeting their nutritional requirements (Machovsky-Capuska et al. 2016a). This potential for flexibility may also explain why, despite variation in habitat usage and distances covered in response to competitive and environmental pressures, different foraging strategies did not affect adult scaled mass. Although specialisation on forage fish and discards has previously been linked to better and poorer body condition respectively at one of these colonies (Grassholm; Votier et al. 2010), a similar result was not found when examining the relationship across multiple colonies (with the exception of Great Saltee; see Fig. S3 in Supplement 1). However, as outlined above, this relationship may vary across years as a consequence of changes in prey field availability and nutritional composition (Hamer et al. 2001, Scales et al. 2014, Tait et al. 2014, Wakefield et al. 2015, Machovsky-Capuska et al. 2016a), and may also be affected by sample sizes. The only other clear distinction was that, at the largest colonies, the scaled mass of individuals tended to be lower. This could be due to competition-driven increases in foraging range impacting on body condition (Lewis et al. 2001), or it may be a strategic decision to reduce wing loading to facilitate longer flights. Whether this has any important effects on longevity or reproductive output remains unknown, particularly as differences may become apparent only under especially unfavourable conditions or when individuals are followed over many years (Annett & Pierotti 1999, Hamer et al. 2007, Lescroel et al. 2010). This is especially likely as long-lived adults maintain a wide safety margin in body mass, prioritising self-maintenance over current provisioning, potentially requiring much longer-term individual based studies to determine fitness effects (Lecomte et al. 2010).

Our findings demonstrate that dietary specialisations can have important consequences for the competitive regimes that individual gannets experience and, at several colonies, although sample sizes were relatively small, this can result in spatial separation of individuals of

409 specialist and generalist foraging strategies. This pattern was seen at both small and large

410 colonies that were located away from shelf breaks, suggesting that intraspecific competitive

411 effects are not the sole contributor to these patterns. For example, interspecific effects may

412 mirror intraspecific interactions at multi-species aggregations, leading to disruption of

413 feeding opportunities, with such interspecific competitive regimes often important in

414 affecting species foraging distributions (Ballance et al. 1997, Ronconi & Burger 2011,

415 Dhondt 2012). The interactions between foraging specialisations and competition are

416 nuanced, and the consequences found here highlight the complexity of examining interacting

417 consequences at large spatial scales.

418 Data archive. Tracking data are available from Birdlife International at

419 http://seabirdtracking.org/mapper/contributor.php?contributor_id1⁄4207. Data for the models

420 presented in Table 2 is included in Supplement 2 at www.int-

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634   Table 1. Fieldwork locations, sample sizes and foraging strategy categorisations of northern gannets. Colony sizes are apparently occupied nests

635   (AON) counted in 2004 except for the Grassholm site, which was surveyed in 2009 (http://jncc.defra.gov.uk/smp/). Retrieved devices are those

636   from which data were successfully recovered. SIA: stable isotope analysis

Colony name	Geographic location	Colony size (AON)	Devices retrieved with multiple complete trips (deployment dates)	Median number of trips ind.$^{-1}$	Individuals sampled for SIA		Generalists	Forage fish specialists	Discard specialists
					Males	Females			
Great Saltee, Ireland	52° 06' N, 06° 37' W	2400	18 (2–19 Jul)	9	13	20	26 (79%)	4 (12%)	3 (9%)
Bull Rock, Ireland	51° 35' N, 10° 18' W	3700	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	27100	16 (7–22 Jul)	7	5	11	11 (69%)	2 (13%)	3 (19%)
Little Skellig, Ireland	51° 46' N, 10° 30' W	29700	9 (11–23 Jul)	7	5	5	6 (60%)	3 (30%)	1 (10%)
Grassholm, Wales, UK	51° 43' N, 05° 28' W	39300	30 (25 Jun–29 Jul)	7	22	18	22 (55%)	8 (20 %)	10 (25%)
Bass Rock, Scotland, UK	56° 05' N, 02° 24' W	55500	25 (26 Jun–2 Aug)	6	14	9	19 (82%)	4 (18%)	0 (0%)

637

638 Table 2. Comparison of mixed models examining the effect of dietary specialisation on
639 northern gannet foraging movement metrics. The top model determined by Akaike's
640 information criterion (AIC) ranking for each metric is presented in **bold**, and the most
641 parsimonious model is marked with * (see 'Materials and methods' for more details). The
642 variance explained by the top model for each metric (and the most parsimonious where
643 relevant) is also presented

Model	ΔAIC compared to top model for each foraging metric		
	Trip distance (km)	Max. 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	0.36*
Sex + colony + dietary type + sex × dietary type	0.38	0.72*	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 most parsimonious*	–	0.284	0.471

644

645 Table 3. Comparison of general linear models examining the effect of dietary specialisation
646 on scaled mass of adult gannets. The top model determined by Akaike's information criterion
647 (AIC) ranking is presented in **bold**, and the most parsimonious model is marked with * (see
648 'Materials and methods' for more details). The variance explained by the top model is also
649 presented

Model	ΔAIC compared to top model
	(scaled mass)
Colony + sex	**0.00***
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

650

651 Fig. 1. Maximum distance travelled from the colony by northern gannets on foraging trips

652 (averaged across all colonies) depends on gannet dietary type and sex (females [F] = dark

653 bars, males [M] = white bars; boxes represent interquartile range and median). Number of

654 individuals within each dietary type: generalist: F = 24, M = 30; forage fish specialist: F = 12,

655 M = 3; discard specialist: F = 6, M = 12

656

657 Fig. 2. Habitat selection function (HSF) and utilisation distribution (UD) plots for different

658 dietary types (generalists = black; forage fish specialists = red; discard specialists = blue) at

659 each of the study colonies. Left hand panels: HSF plots show how usage changes with the

660 level of competition at each colony. Solid lines: the smoother from the fitted model,

661 reflecting the predicted strength of choice of those competitive conditions for the different

662 foraging strategies; dashed lines: 95% confidence intervals. Note the x-axis for competition

663 has been reversed so that the highest levels of competition (closer to the colony) appear to the

664 left. Right hand panels: maps showing the 50% (solid line) and 95% (dashed line) UDs of

665 different dietary types