

Individual seabirds show consistent foraging strategies in response to predictable fisheries discards

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Abstract:	<p>Current fishing methods often generate huge quantities of dead biomass that is returned to the sea in the form of discards. This practice produces readily available clumped resources for scavengers such as seabirds, but in the face of declining stocks and via policy change, the amount of discards produced is set to decline in the future. To understand how discards have influenced seabird foraging in the past and how birds may respond to future change requires studies examining consistent individual foraging choices. There is increasing evidence that populations may be composed of generalist or specialist foragers and this is key to the population's ability to adapt to change. Here we test for consistent individual foraging behaviour of northern gannets (<i>Morus bassanus</i>) in relation to fishing vessels and examine consequences of scavenging behaviour in terms of foraging effort and body condition. Using a combination of bio-logging devices (GPS and Time Depth Recorders) with high resolution GPS data acquired through vessel monitoring systems on fishing boats, we examined the overlap between birds and fisheries. We found that during repeat foraging trips in the same breeding season, gannets regularly foraged at fishing boats but there were clear among individual differences in the extent of fisheries overlap. Furthermore, we show for the first time that these differences represent consistent strategies – individual differences in scavenging were highly repeatable across multiple trips. However, despite these differences, we found no differences in foraging effort or body condition between scavengers and non-scavengers. Moreover, scavenging strategy did not influence diving behaviour or vary by sex. Scavenging on discards appears to be a strategy employed consistently by a subsection of</p>

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1 **Individual seabirds show consistent foraging strategies in response to**
2 **predictable fisheries discards**

3

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16

17

18 **Abstract**

19 Current fishing extraction methods often generate huge quantities of dead or dying biomass
20 that is returned to the sea in the form of discards. This practice produces a readily available
21 clumped resource for many scavengers such as seabirds, but in the face of declining stocks
22 and via policy change, the amount of discards produced is set to decline in the future. To
23 understand how discards have influenced seabird foraging in the past and how birds may
24 respond to future change requires studies examining consistent individual foraging choices.
25 There is increasing evidence that populations may be made up of generalist or specialist
26 foragers and this is key to the population's ability to adapt to change. Here we test for
27 consistent individual foraging behaviour of northern gannets (*Morus bassanus*) in relation to
28 fishing vessels and examine consequences of scavenging behaviour in terms of foraging effort
29 and body condition. Using a combination of bird-borne bio-logging devices (GPS and Time
30 Depth Recorders) with high resolution GPS data acquired through vessel monitoring systems
31 on fishing boats, we examined the overlap between birds and fisheries. We found that during
32 repeat foraging trips in the same breeding season, gannets regularly foraged at fishing boats
33 but there were also clear among individual differences in the extent of fisheries overlap.
34 Furthermore, we show for the first time that these differences represent consistent strategies –
35 individual differences in scavenging were highly repeatable across multiple trips. However,
36 despite these differences, we found no differences in foraging effort or body condition
37 between scavengers and non-scavengers. Moreover, scavenging strategy did not appear to
38 influence diving behaviour or vary by sex. Scavenging on discards appears to be a strategy
39 employed consistently by a subsection of the population, and future work should examine
40 what causes these individual differences and explore possible demographic and fitness
41 consequences in light of global changes to fish stocks and fisheries management.

42

43 Keywords

44 Specialisation, personality, GPS tracking, intra-individual variability, consistent individual
45 differences, alternative foraging strategies, discards, fisheries, seabird

46

47 **Introduction**

48 Commercial fisheries have changed the structure and functioning of marine ecosystems
49 worldwide (Lewison et al. 2004, Smith et al. 2011). These changes can lead to cascading
50 effects throughout the ocean, with consequences for many higher predators (Furness 2003,
51 Pikitch 2012). While these effects are often deleterious, such as accidental seabird bycatch
52 (Brothers et al. 1999, Weimerskirch et al. 2000), fisheries also provide an important food
53 subsidy for large numbers of scavengers across the globe, in the form of discarded fish and
54 offal (Furness 2003, Votier et al. 2004a, Bicknell et al. 2013). Foraging on discards allows
55 scavengers, such as some seabirds, to supplement and broaden their diet by utilising prey that
56 would otherwise be unavailable (Furness 2003, Votier et al. 2004a, Bicknell et al. 2013).
57 Concerns about the parlous states of global fish stocks, as well as the wasteful and potentially
58 deleterious impact of discarding, have led to widespread changes to discarding practices.
59 These changes include an introduction of more selective gears to reduce bycatch, and a policy
60 to retain 100% of catch (Council of the European Union 2013). Despite the clear benefits of
61 such measures to fish stocks (Catchpole et al. 2005), the ecosystem-wide implications of a
62 discard ban, particularly for seabirds, are more difficult to predict and warrant further study
63 (Bicknell et al. 2013).

64

65 Seabirds are well known to forage at fishing vessels, with species of Procellariiformes,
66 Sulidae and Laridae being conspicuous consumers behind trawlers (Garthe et al. 1996,
67 Furness 2003, Bicknell et al. 2013, Votier et al. 2013). While discards create a clumped,
68 easily accessible resource for these species, the uncertain future of this practice emphasises

69 the need to clarify how such resources are divided among individuals, populations and species
70 (Bicknell et al. 2013). Recent work has highlighted that individuals differ in their attendance
71 at vessels and the quantity of discards they consume (Votier et al. 2010, Granadeiro et al.
72 2011, Torres et al. 2011, Votier et al. 2013, Granadeiro et al. 2014). This phenomenon may
73 be a manifestation of individuals opportunistically exploiting fishing discards when they
74 encounter them (i.e. they may be opportunistic generalists), or it may be evidence that
75 subsections of the population specialise on discarded fish (i.e. they may be specialists).

76

77 The persistence of generalists and specialists in nature is widely attributed to the degree of
78 stability of available resources (Westerberhard 1989). Generalist foragers display greater
79 phenotypic plasticity, which enables them to respond more rapidly to fluctuations in the
80 environment (Westerberhard 1989, Robinson et al. 1996, Svanback & Schluter 2012).
81 Generalists are thus favoured in unpredictable and unstable environments. However,
82 specialisation can be highly advantageous as individuals can decrease search and handling
83 costs and reduce their niche overlap with other individuals, minimising competition (Bolnick
84 et al. 2003, Araujo et al. 2011). While this strategy may be favoured in stable environments,
85 specialisation strongly contributes to extinction risk if it is coupled with reduced plasticity in
86 behaviour at the population level (Mitter et al. 1988, Biesmeijer et al. 2006).

87

88 Foraging specialisations are widespread in seabirds (Votier et al. 2004b, Bearhop et al. 2006,
89 Woo et al. 2008, Patrick et al. 2014), and their prevalence in nature is thought to emerge as a
90 result of the broad-scale predictability in marine resources (Weimerskirch 2007, Scales et al.
91 2014). Foraging behaviours in seabirds have also evolved in the presence of persistent
92 anthropogenic food sources (McCleery & Sibly 1986, Annett & Pierotti 1999, Votier et al.
93 2004b, Navarro et al. 2009, Navarro et al. 2010, Votier et al. 2010, Granadeiro et al. 2011,

94 Torres et al. 2011, Oro et al. 2013, Granadeiro et al. 2014), suggesting consistency can
95 develop rapidly in response to newly available prey. Furthermore, foraging specialisations may
96 represent consistent individual differences or “personality differences” (Reale et al. 2007) and
97 there is increasing evidence that niche segregation itself may lead to the emergence of such
98 personalities (Bergmuller & Taborsky 2010). The union between foraging specialisations and
99 animal personality is particularly important as there is strong evidence that personality
100 differences are heritable (e.g. Dingemanse et al. 2002, Sinn et al. 2006) and this heritability
101 has recently been demonstrated in seabirds (Patrick et al. 2013).

102

103 There is some evidence of among individual differences in the use of discards by seabirds
104 (Votier et al. 2004b, 2010), but it is unclear the extent to which these represent consistent
105 differences in individual tactics. The only previous attempt to quantify the consistency of
106 foraging strategies in terms of at-sea association around fishing vessels found no support for
107 specialisation (Granadeiro et al. 2014), although the study examined behaviour over the
108 Patagonian Shelf where fishing effort is low and patchy (Granadeiro et al. 2011). By contrast,
109 in other parts of the world fishing effort tends to be more intensive and consistent, which
110 could lead to the emergence of consistent individual scavenging tactics. In the Celtic Sea, for
111 example, fishing boats are found at very high density, and tend to be consistent in time and
112 space (Witt & Godley 2007, Campbell et al. 2014). The intensity and wide-spread
113 distribution of fishing vessels makes this an ideal test of the hypothesis that specialisation is
114 more likely to emerge under stable and predictable conditions.

115

116 In this study, we use bird-borne GPS loggers and time depth recorders (TDRs) to reconstruct
117 fine-scale foraging behaviour of chick-rearing northern gannets (*Morus bassanus*) from a
118 single large colony and relate this to fishing vessel activity in the Celtic Sea from the vessel

119 monitoring system (VMS). Using repeat foraging trips from the same individuals to examine
120 consistent sex-specific and individual differences in seabird-fishery interactions, we test the
121 following hypotheses: (i) Individual gannets differ in the extent to which they overlap with
122 fishing boats; (ii) These differences are consistent over repeat foraging trips; (iii) A subsection
123 of the population accounts for this repeatability, specialising in targeting fishing vessels. We
124 then extend these analyses to assess the costs and benefits to any variation by testing the
125 following predictions: (iv) birds that forage at boats exhibit changes to their foraging
126 behaviour, investing less energy in foraging, and; (v) birds that forage at boats show poorer
127 body condition compared to those that do not.

128

129 *Materials and methods*

130 *Data collection*

131 Fieldwork was carried out on Grassholm, Wales, UK (51°43'N, 05°28'W) during chick-
132 rearing in July and August 2010. Approximately 40,000 pairs of gannets breed here annually
133 and 26 individuals were fitted with i-gotU GPS loggers (Mobile Action Technology; mass
134 30g) and ten birds with an additional G5 time-depth recorder (TDR; CEFAS technology; mass
135 6g). All devices were attached to the central tail feathers using TESA tape (Tesa Tape Inc).
136 GPS loggers were programmed to record locations every two minutes, and TDRs had a
137 recording frequency of 10Hz once submerged. 20 birds had usable GPS data (19 of known
138 sex) and of these, 7 birds (6 of known sex) had complete TDR dive data. Capture and
139 handling time of birds was <10 minutes. Previous studies have found no effect of larger
140 devices on foraging trip duration (Hamer et al. 2009) and in the present study, no individuals
141 abandoned chicks during the study period and we have no evidence that devices changed
142 birds' foraging behaviour. Blood samples were collected from the tarsal vein of all
143 individuals, under licence from the UK Home Office, for subsequent molecular sexing.

144 Samples were spun in a centrifuge at 14,000 rpm for approximately 10 minutes to separate red
145 blood cells and plasma before being stored on ice. DNA was extracted from 2ml of red blood
146 cells using the ammonium acetate protocol based on Bruford *et al.*(1998). Individuals were
147 sexed using 2550F (Fridolfsson & Ellegren 1999) and 2757R (Griffiths et al. 1998) primers
148 (K. Griffith, pers. comm; Table S1).

149

150 ***Fisheries activity***

151 High-resolution data on the location of commercial fishing vessels are available from the
152 vessel monitoring system (VMS). At the time of the study data, were available describing the
153 location, in UK waters, of vessels >15m of all nationalities at a temporal resolution of ± 2
154 hours. Data from Irish waters included only UK vessels and so were excluded (8% of all
155 locations; see Table S2 for details of excluded data). The Centre for Environment, Fisheries
156 and Aquaculture Science (CEFAS) conducted VMS data filtering and provided an
157 anonymised output, which was used to calculate measures of fishing activity. A generic
158 speed filter was applied to identify and remove points where boats may not have been actively
159 fishing. This is important because gannets tend not to be attracted to fishing vessels that are
160 either steaming or drifting (Bodey et al. 2014). As vessel locations were available only every
161 2 hours, this introduced uncertainty into the interim positions of these boats. While simple
162 straight line or curvilinear interpolation can be employed in such circumstances, its accuracy
163 depends on a number of assumptions that we were not able to test (Torres et al. 2011).
164 Accordingly, we instead used 30 km buffers (estimated maximum distance a boat could move
165 in two hours) around exact known locations with a two-hour time window, to provide a
166 conservative estimate of vessel location.

167

168 Because VMS is restricted to vessels >15m and there may be some Illegal, Unreported and
169 Unregulated fishing, we sought an independent assessment of fisheries interactions. Data
170 collected from small bird-borne cameras (See Votier et al. 2013 for methods) deployed in
171 2011 showed that 84/89 (94%; S. Votier, Unpub. data) of locations known to be with a vessel
172 from photographs were also categorised as overlapping with fisheries using our VMS
173 methods described above. Therefore we can be confident that VMS provides a very accurate
174 representation of gannet/fishery interactions.

175

176 *Analysis*

177 *Overlap between gannets and fisheries*

178 The spatial positions of individual gannets were extracted from GPS data (hereafter “gannet
179 positions”) and overlaid with VMS data to determine the extent of overlap between gannets
180 and fishing vessels. We used three different data sets (Figure 1):

181

182 (i) *Complete tracks.*

183 As birds may feed throughout foraging trips (Hamer et al. 2009; Figure 1), we first
184 used gannet positions from complete trips (Figure 1b). We removed all points when
185 birds were on the water (this behaviour was identified using a speed threshold of
186 5kmh^{-1}) and positions at night, when birds do not feed (Hamer et al. 2000). We also
187 excluded partial foraging trips and any points within 1km of the colony, to avoid
188 times when birds were at the nest.

189 (ii) *Area restricted search zones (ARSZ).*

190 Centrally-placed foraging trips typically include commuting behaviour, where there
191 may be strong spatial and temporal auto-correlation in the data. To overcome such
192 problems, we identified areas of reduced speed and increased turning rate where

193 individuals spent prolonged periods (hereafter ARSZ). These zones are strongly
194 associated with increased foraging effort in a number of marine predators, including
195 gannets (Hamer et al. 2009). We identified these areas by calculating residence times
196 at each GPS location along all foraging tracks (Barraquand & Benhamou 2008).
197 Residence time estimates the amount of time a bird spends in a circle of given radius
198 (here 30km). We favour this method above others (e.g. first-passage time; Pinaud and
199 Weimerskirch. 2005), because in the method we used there is no subjectivity between
200 individual measures, ensuring that individual differences are due to actual behavioural
201 variation and not analytical techniques. These data were available for all birds and
202 we selected GPS locations where the residence time was in the upper quartile, and
203 used these locations as ARSZ. For this analysis, we removed all points when birds
204 were on the water, night positions, partial foraging trips and any points within 1km of
205 the colony (Figure 1c).

206 (iii) *Dive locations*

207 For 7 birds with simultaneous GPS and TDR data, we interpolated GPS tracks to a
208 resolution of 1 second using a cubic spline interpolation, and matched these temporal
209 data to those from the TDR. Once we had matched the time stamp from the GPS and
210 TDR, we extracted the dive positions from the GPS data (Figure 1d).

211

212 Across these three sets of data we determined whether or not every gannet position was within
213 30km and ± 2 hours of any fishing vessel based on VMS data. A gannet position was scored
214 as; 0 = no boats were present or 1 = at least one boat was present.

215

216 *Between individual variation in fisheries overlap*

217 For each bird, the total number of positions with a boat present per trip was divided by the
218 total number of positions per trip, to give the proportion of time spent at fishing vessels
219 (bounded by zero and one). Individual and sex-specific differences in this response variable
220 were then examined in a general linear mixed model with a Gaussian error structure, with
221 individual bird ID and then sex fitted as a fixed effect in models. While our data could be
222 modelled with a binomial error structure, this weights longer foraging trips more heavily and
223 we did not want this. Instead the proportion of points at fishing vessels approximated well to
224 a Gaussian error structure. We were unable to fit bird ID and sex in the same model due to
225 the nature of these variables. We tested for the significance of effects by using ANOVA
226 comparisons of models with and without bird ID or sex. Fitting bird ID as a fixed effect with
227 sex led to a rank deficient model where we could not estimate all coefficients, so we were
228 constrained to fit each effect in turn.

229

230 *Are individuals repeatable in their overlap with fisheries?*

231 We estimated individual repeatability (r) in fishery overlap by calculating how much of the
232 variation in time spent at fishing vessels that was explained by individual behaviour. We
233 achieved this by running a general linear mixed model with bird ID as a random effect and no
234 fixed effects (Nakagawa & Schielzeth 2010; Table 1). This repeatability can be thought of as
235 an average level of specialisation among individuals within the population.

236

237 *Do individuals differ in the level of specialisation in their use of fishing vessels?*

238 To examine differences in the degree of specialisation at the individual-level, we classified all
239 trips as “with a boat” or “not with a boat” based on the presence of a vessel in an ARSZ. We
240 then calculated the proportion of birds that were always at vessels (specialists on discards),

241 never at vessels (specialists on natural prey) or a mixture of the two (generalists). This is a
242 metric of intra-individual variability.

243

244 *Influence of fishery interactions on foraging effort*

245 To determine whether association with fishing vessels influenced foraging effort, we
246 calculated the following metrics: (a) trip duration (hours), (b) proportion of time spent flying
247 during daylight (hours; binomial), (c) maximum distance from colony (km; log transformed to
248 conform to the assumptions of normality; maximum range), and for a sub-sample of 7 birds
249 with dive data: (d) the number (Poisson) and (f) the maximum vertical depth of dives reached
250 per individual dive. These metrics were each fitted as the response variable in a linear mixed
251 model with an estimate of average fisheries overlap and sex as fixed effects and bird ID as a
252 random effect (Table 1). Response variables had a Gaussian error distribution except when
253 stated otherwise. Trip ID was also included as a random effect for maximum vertical depth
254 of dive, as there were multiple dives per trip. Average fisheries overlap was calculated using
255 gannet positions from ARSZ because dive data were available for only a small subset of
256 individuals. The proportion of points with boats present per trip was divided by the total
257 number of points per trip to give a value from 0 (no overlap with vessels) to 1 (all ARSZ
258 overlap with vessels).

259

260 *Influence of fishery interactions on body condition*

261 The maintenance of body condition has important fitness consequences (Velando & Alonso-
262 Alvarez 2003), and so we examined whether or not there were differences in the body
263 condition of gannets depending on whether they largely scavenged at fishing vessels or not.
264 Body condition was estimated using a general linear model, with mass as the response and

265 wing, tarsus and bill as fixed effects. Sex and the average overlap with fisheries were fitted as
266 fixed effects.

267

268 ANOVA comparisons of models with and without terms of interest were used to test the
269 significance of main effects (Table 1). Fixed effects with a significance of $p < 0.10$ were
270 maintained in models (Except for individual differences; see above). Analyses were
271 conducted in Matlab (R2009b, Mathworks), R 2.11.1 (R Development Core Team), Free
272 Pascal 1.0.12 and ArcGIS 9.3 (ESRI, USA).

273

274 **Results**

275 Foraging tracks were obtained for 20 individuals, with three repeat trips from nine
276 individuals, four repeats from eight individuals, five repeats from one individual and seven
277 repeats from two individuals. Fisheries data were available for all foraging trips.

278

279 **Overlap between gannets and fisheries**

280 There were strong differences among individuals in the overlap with fisheries, ranging from
281 4% to 100% overlap during a single trip (Table 2; Electronic supplementary material Table
282 S2). These differences in the extent of interaction with vessels were highly repeatable within
283 individuals (measured over a period of 6.14 – 8.36 days), especially at dive sites (differences
284 between individuals: $F_{6,22} = 23.10$; $p < 0.001$; Table 2; repeatability between individuals: $r =$
285 0.88 ± 0.12 ; $p < 0.001$; Table 2; Figure 2) indicating that these differences represent
286 consistent individual strategies. 60% of birds (4 of 6 females; 8 of 14 males) overlapped with
287 boats on all trips and only 10% of birds (none of 6 females; 2 of 14 males) never overlapped
288 with vessels. 30% of birds (2 of 6 females; 4 of 14 males) had some foraging trips with boats
289 and some without, suggesting that 70% of our population showed some degree of

290 specialisation, while 30% were true generalists. There was no evidence of sex differences in
291 the overlap with fisheries (Table 2).

292

293 *Influence of fishery interactions on foraging effort*

294 All measures of foraging effort were highly variable between individuals (Table 2). However,
295 overlap with fishing vessels was not a good predictor of trip duration ($\chi^2_1 = 0.20$; $p = 0.65$;
296 Table 2), proportion of time spent flying ($\chi^2_1 = 0.09$; $p = 0.76$; Table 2), maximum range
297 (maximum distance from colony: $\chi^2_1 = 3.18$; $p = 0.07$; Table 2), nor the number ($\chi^2_1 = 2.28$; p
298 $= 0.13$; Table 2) or depth of dives ($\chi^2_1 = 1.94$; $p = 0.16$; Table 2). There were no sex
299 differences in trip duration ($\chi^2_1 = 0.09$; $p = 0.78$; Table 2), proportion of time spent flying
300 maximum range ($\chi^2_1 = 1.39$; $p = 0.24$; Table 2), maximum range ($\chi^2_1 = 1.51$; $p = 0.22$; Table
301 2) nor the number ($\chi^2_1 = 0.08$; $p = 0.77$; Table 2) or depth of dives ($\chi^2_1 = 2.80$; $p = 0.09$; Table
302 2).

303

304 *Influence of fishery interactions on body condition*

305 There was no relationship between body condition and the degree of association with fishing
306 vessels ($F_{5,13} = 0.00$; $p = 0.96$).

307

308 **Discussion**

309 In this study, we show that during multiple foraging trips from the same birds, there is
310 repeatable overlap between foraging gannets and fishing vessels. Our results support previous
311 studies suggesting between individual variation in the degree of association between seabirds
312 and fisheries (Votier et al. 2010, Granadeiro et al. 2011, Torres et al. 2011, Granadeiro et al.
313 2014), but importantly we demonstrate that these differences, over 3-7 repeat trips (6.14 –
314 8.36 days), represent consistent individual foraging strategies (i.e. specialisation), with 70%

315 of birds being specialists. Foraging repeatability was particularly strong at dive sites (See
316 Bell et al. 2009 for a review of behavioural repeatabilities), which may be related to the fact
317 that this is our most accurate measure of foraging location. We found no evidence of sex
318 differences in the overlap with fishing boats and there was little evidence to suggest that
319 overlap with fisheries results in changes to foraging effort or diving behaviour. These results
320 compliment previous dietary studies (e.g. Annett & Pierotti 1999, Votier et al. 2004b, Votier
321 et al. 2010) showing individual differences in discard consumption and highlight the
322 importance of individual foraging strategies.

323

324 **Individual foraging specialisation at fishing vessels**

325 Consistent individual diet and foraging strategies are common among seabirds (e.g. Votier et
326 al. 2004b, Bearhop et al. 2006, Patrick et al. 2014). However, to date, they have mainly been
327 reported in natural systems (but see also McCleery & Sibly 1986, Annett & Pierotti 1999,
328 Votier et al. 2004, Navarro et al. 2009, Navarro et al. 2010, Votier et al. 2010, Granadeiro et
329 al. 2011, Torres et al. 2011, Oro et al. 2013, Granadeiro et al. 2014) and here we provide
330 support that individual strategies may evolve when birds use anthropogenic resources.
331 Previous work has shown that feeding on discards can be a highly specialised strategy, with
332 consequences for fitness (e.g. Annett & Pierotti 1999). In this study, we demonstrate that
333 such specialisation in diet is coupled with behavioural specialisation at the individual level: in
334 this population, assuming birds do not differ in encounter with boats by chance, 70% of birds
335 are behaviourally specialised to foraging with or without fishing boats. Although our data
336 were collected over a single season, previous suggestions that such prey choice (Annett &
337 Pierotti 1999) and personality-mediated foraging behaviour (Patrick and Weimerskirch 2014;
338 Patrick et al. 2013) could have a genetic basis raise interesting questions about foraging
339 plasticity between years. This leads to the prediction that individuals may demonstrate

340 limited plasticity potentially constraining an individual's ability to change strategies and
341 future work should focus on the consistency in behaviour over years and the potential
342 selection consequences for subsections of the population undertaking different strategies.

343

344 A key assumption is that VMS data offers an accurate representation of fishing activity in the
345 Celtic Sea. The VMS data only covered vessels >15m during the study period and may
346 therefore have missed interactions with smaller vessels. However, analysis of large numbers
347 of images from gannet-borne cameras reveals that these birds tend only to be attracted to large
348 vessels in the Celtic sea such that this is unlikely to be a shortcoming (Votier et al. 2013).
349 Analysis of camera data almost meant the possibility that gannets may also associate with
350 illegal, unreported and unregulated fisheries is unlikely.

351

352 *Sex specific differences in fishery interactions*

353 In this study we found no evidence of sex-specific differences in the extent to which gannets
354 associated with fishing vessels. Previous work has shown sex-related differences in
355 scavenging behaviour of seabirds, although this appears to vary among species and over time.
356 For instance, a study on gannets from the same colony in 2006 showed, using stable isotope
357 mixing models, that males consumed a higher proportion of discarded whitefish compared
358 with females (Stauss et al. 2012). In addition, analysis of images from bird-borne digital
359 cameras on gannets in 2011 showed that 80% of male ARSZ were associated with fishing
360 vessels, whereas this proportion was only 30% for females (Votier et al. 2013). In contrast,
361 Torres et al. (2011) found no difference in the extent to which male and female white-capped
362 albatrosses *Thalassarche steadi* interacted with fishing vessels, and the same is true of black-
363 browed albatross *T. melanophrys* (Patrick & Weimerskirch 2014). Taken together these
364 results suggest that the degree of attraction to fishing vessels varies not only within but also

365 among species and populations, highlighting the need for studies into factors influencing
366 variation in sex-specific foraging behaviour over time. For instance, some personality types
367 are more plastic in their behaviour (Dingemanse et al. 2010) and individuals specialising on
368 one type of prey may be more plastic than others.

369

370 **Does overlap with fishing boats reduce foraging effort?**

371 We found little evidence that the overlap with fishing vessels correlated with differences in
372 foraging behaviour. Previous research indicated that gannets feeding more on discards were
373 in poorer condition compared with others during 2006 (Votier et al. 2010), suggesting that the
374 costs and benefits of interactions with fishing vessels may vary with time. We found no
375 evidence to support the hypothesis that foraging at vessels results in fewer dives. However,
376 we were able to collect dive data from only 7 individuals and so while we have many repeat
377 dives per individual, giving us confidence in our within-individual measures, our power to
378 assess between-individual differences is limited. Indeed, Figure 2 suggests that birds
379 foraging naturally may dive more frequently than those feeding at fishing vessels and future
380 work should focus on obtaining more dive data to allow a comparison between individuals in
381 this respect.

382

383 **Conclusions**

384 Our results indicate that individual differences in the extent to which gannets forage at fishing
385 vessels are consistent over time and therefore may be considered a form of foraging
386 specialisation. The mechanisms underlying these individual strategies and their plasticity are
387 poorly understood but may have population-level implications if subsections of the population
388 are forced to change prey in the face of changes in the availability of discards via reform to
389 the EU Common Fisheries Policy (Bicknell et al. 2013). While we strongly support changes

390 to current discarding practices, we suggest more attention should be given to the potential loss
391 of behavioural variation from the population, linked to the ability to respond to a drastic
392 changes to the environment. Such effects could have ecosystem-wide consequences and we
393 must ensure the system is resilient to this major change in the way we manage our seas
394 (Diamond & Beukers-Stewart 2011, Bicknell et al. 2013).

395

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407 Table 1: Summary of analyses conducted in this study. Analyses are grouped as they are in the text and full details of the models are given here.

Group	Analysis	Response	Error Distribution	Fixed effects	Random effects
1) Overlap with fisheries	Individual differences	Total trip: Proportion of gannet positions with boat	Gaussian	Bird ID / Sex	
		ARSZ: Proportion of gannet positions with boat	Gaussian	Bird ID / Sex	
		Dives: Proportion of dives with boat	Gaussian	Bird ID / Sex	
	Individual repeatability	Total trip: Proportion of gannet positions with boat	Gaussian		Bird ID
		ARSZ: Proportion of gannet positions with boat	Gaussian		Bird ID
		Dives: Proportion of dives with boat	Gaussian		Bird ID
2) Foraging behaviour	a) Trip duration	Trip duration	Gaussian	Average fisheries overlap + Sex	Bird ID
	b) % Time spent flying	Proportion of time spent flying	Binomial	Average fisheries overlap + Sex	Bird ID
	c) Maximum range	Maximum range	Gaussian	Average fisheries overlap + Sex	Bird ID
	d) Number dives	Number dives	Poisson	Average fisheries overlap + Sex	Bird ID
	e) Maximum vertical dive depth	Maximum vertical dive depth	Gaussian	Average fisheries overlap + Sex	Bird ID + Trip ID
3) Body condition	Body Condition	Mass	Gaussian	Average fisheries overlap + Sex + Wing + Tarsus + Bill	

408

409

410 Table 2: A summary table of the results from the main models in the paper. The raw data is described and the maximum range of values found in
 411 each data set. Results examining individual and sex differences are also given and significant results highlighted in bold and those maintained in
 412 the model ($p < 0.1$) in italics.

Group	Analysis	Response	No. birds (Sex effect)	No. trips	No. data points	Range (per trip)	Bird ID	Average fishing overlap	Sex
1) Overlap with fisheries	Individual differences	Total trip: Proportion of gannet positions with boat	20 (19)	78	23988	0.04 – 1.0	$F_{19,55} = 6.47$; $p < 0.001$		$F_{1,70} = 0.67$; $p = 0.41$
		ARSZ: Proportion of gannet positions with boat	20 (19)	75	4279	0.00 – 1.00	$F_{19,55} = 3.12$; $p < 0.001$		$F_{1,70} = 0.24$; $p = 0.62$
		Dives: Proportion of dives with boat	7 (6)	23	957	0.00 – 1.00	$F_{6,22} = 23.10$; $p < 0.001$		$F_{1,18} = 2.72$; $p = 0.12$
	Individual repeatability	Total trip: Proportion of gannet positions with boat	20	78	23988	0.04 – 1.00	$r = 0.60 \pm 0.10$; $p < 0.001$		
		ARSZ: Proportion of gannet positions with boat	20	75	4279	0.00 – 1.00	$r = 0.37 \pm 0.13$; $p = 0.005$		
		Dives: Proportion of dives with boat	7	23	957	0.00 – 1.00	$r = 0.88 \pm 0.12$; $p < 0.001$; Fig. 2		
2) Foraging behaviour	a) Trip duration	Trip duration	20 (19)	75	4279	2.74 - 97.27 hrs		$\chi^2_1 = 0.20$; $p = 0.65$	$\chi^2_1 = 0.09$; $p = 0.78$
	b) % time spent flying	Proportion of time spent flying during daylight	20 (19)	75	4279	0 – 93%		$\chi^2_1 = 0.09$; $p = 0.76$	$\chi^2_1 = 1.39$; $p = 0.24$
	c) Maximum range	Maximum range	20 (19)	75	4279	29.03 - 653.68 km		$\chi^2_1 = 3.18$; $p = 0.07$	$\chi^2_1 = 1.51$; $p = 0.22$
	e) Number dives	Number dives	7 (6)	23	957	1 - 130 dives		$\chi^2_1 = 2.28$; $p = 0.13$	$\chi^2_1 = 0.08$; $p = 0.77$
	f) Maximum vertical dive depth	Maximum vertical dive depth	7 (6)	23	957	0.5 - 22.18m		$\chi^2_1 = 1.94$; $p = 0.16$	$\chi^2_1 = 2.80$; $p = 0.09$
3) Body condition	Body Condition	Mass	20 (19)	NA	NA			$F_{5,13} = 0.00$; $p = 0.96$	$F_{4,14} = 3.61$; $p = 0.08$

413

414

415 Figure 1: Methods used to select data from GPS tracking information to produce estimates of
416 gannet foraging areas. a) Solid circles (White): All recorded GPS locations. This was not
417 used in any analysis but is shown to demonstrate the raw data. Arrows show the direction of
418 movement; b) Solid circles (Green): Complete foraging track: all recorded points shown in
419 (a), filtered to exclude points at night or on the water, when birds do not forage; c) Solid
420 circles (Red): “ARSZ” – points from (b) with a residence time in the upper quartile (see text
421 for methods); d) Solid circles (Yellow): “Dive locations” – points from (b) where dives
422 occurred, extracted from time depth recorder data. In plots b-d all GPS locations are plotted
423 as small black points to show the route taken by the bird. Online version only in colour.

424

425 Figure 2: Individual consistency in association with vessels. The number of dives in the
426 presence or absence of fishing vessels for seven individual gannets, across all foraging trips.
427 Pale bars (yellow) show diving when a fishing vessel is nearby and dark bars (blue) show
428 diving in the absence of a fishing vessel. When bars are one colour, this represents an
429 individual that engages in only one strategy. Birds 1-2 dive mainly around vessels, birds 3 -4
430 have a mixed strategy and birds 5-7 dive mainly away from boats.

431

432 Figure 3: Three examples of the overlap between foraging gannets and fisheries over
433 sequential tracks. Points where birds overlapped with fisheries are shown by large circles and
434 straight lines show points where birds and boats did not overlap or excluded points (see
435 methods). Shades show different foraging trips. a) A bird that has a specialist strategy and
436 shows limited overlap with fishery activity. b) A bird that is also a specialist but overlaps
437 with a fishing vessel throughout repeated trips. c) A bird that has a generalist strategy, with
438 some dives occurring within 30km of a fishing vessel and some without a vessel. To

439 preserve vessel anonymity, there is no scale or location information on these maps.

440

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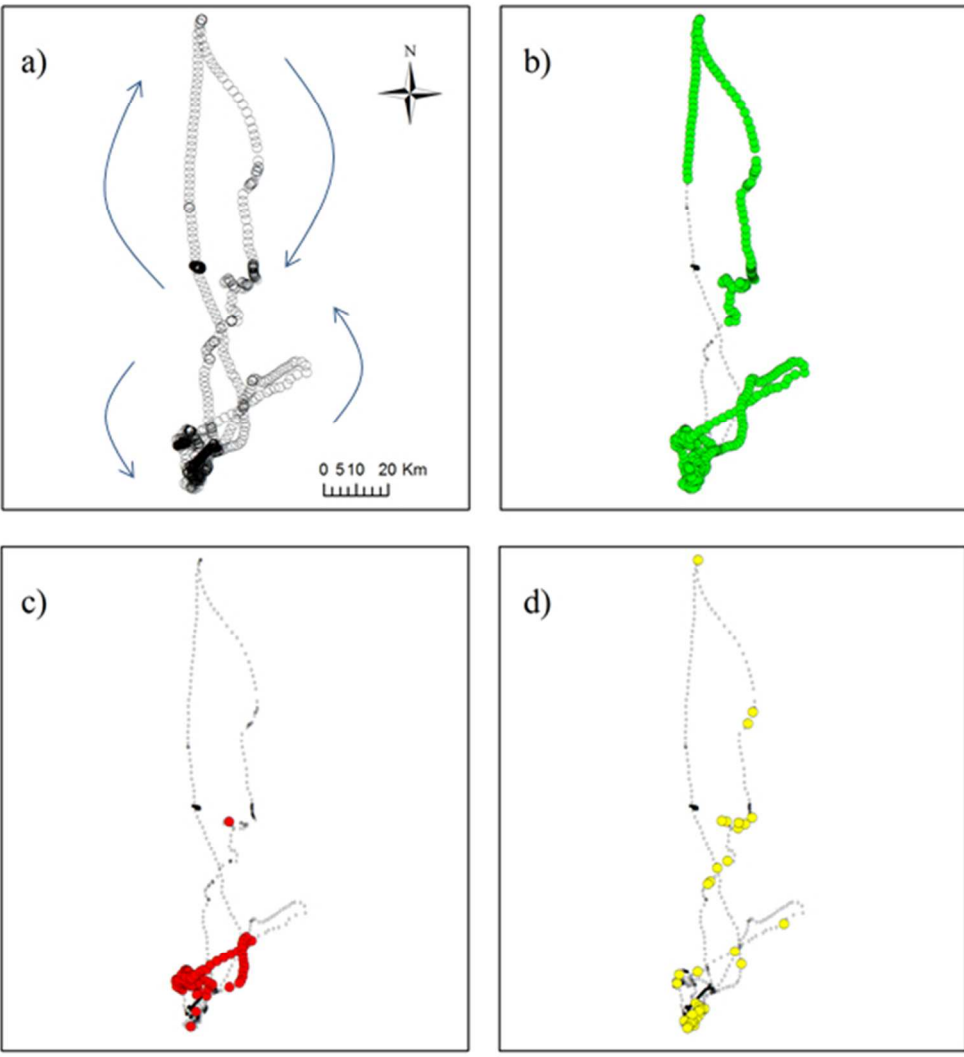
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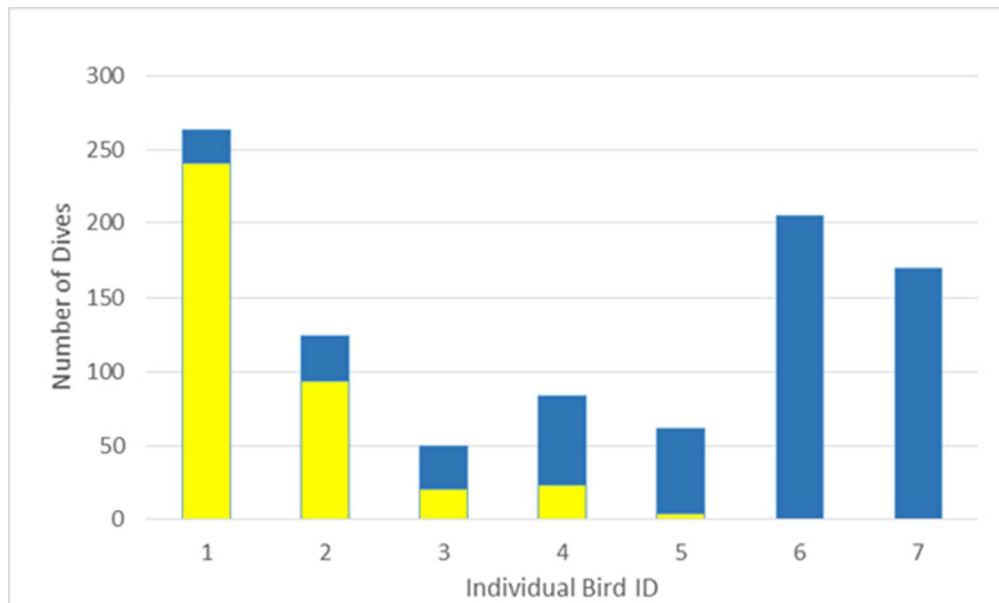
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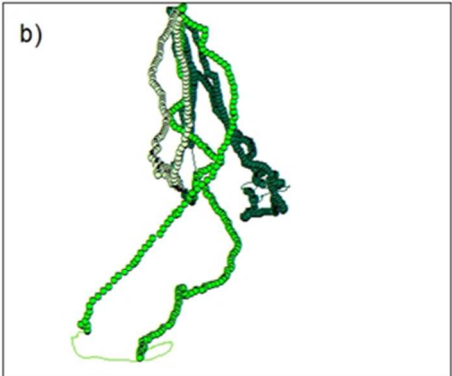


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1 **Electronic supplementary material**2 **Methods**

3 Table S1. The conditions and reagents for sexing individual gannets (K. Griffiths Pers.

4 Comm.)

Primers	2550F 5' GTT ACT GAT TCG TCT ACG AGA -3' 2757R 5' AAT TCC CCT TTT ATT GAT CCA TC -3'
PCR reagents	For each 10ul 2ul DNA (10-100ng/ul) 1ul Qiagen Buffer 1ul Qiagen MgCl ₂ 0.2 ul Qiagen ready mixed dNTP 0.1 ul Qiagen taq 0.124 ul 2550F 0.116 ul 2757R water to make up to 10ul (5.46 ul)
PCR profile	94°C for 2 mins 53°C for 1 min 72°C for 1 min x30 cycles 94°C for 45 secs 49°C for 1 min 72°C for 5 mins 12°C pause
Gel	2% agarose with TDE, 1h30 mins, 110 volts, 110 A.

5

6

7 **Analysing the overlap between fisheries and gannet locations.**

8 Table S2: GPS data excluded from the analysis as it was outside the study area.

	Females	Males	Total
GPS tracking data			
Number of gannet locations	6961	15845	22806
Number of gannet locations outside study area (removed)	499 (7%)	1275 (8%)	1774 (8%)

9

10 **Modelling the overlap between gannets and fisheries**

11 Gannets = 20

12 Trips = 78

13 Total GPS Points (p) = 23988

14

15 **Step 1**

16 For every point, p → Measure distance to every fishing boat (m)

17 → Compare timestamps (t)

18 → if $m < 30 \text{ km}$ & $t < 2 \text{ hours}$

19 overlap = 1

20 Else overlap = 0

21 Output = Overlap score for all 23,988 GPS positions

22 **Step 2**

23 For each of the 78 trips: → Total number of GPS positions

24 → Total number of GPS positions with overlap = 1

25 Output = Summary statistics for each trip used in binomial models

26

27 These two steps were repeated on restricted data sets including only GPS positions where the
28 residence time was in the upper quartile ($n = 4279$ positions) or exact dive locations ($n = 957$
29 positions).

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