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1 # GPS tracking reveals rafting behaviour of Northern

2 # Gannets (*Morus bassanus*): Implications for

3 # foraging ecology and conservation

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21 **SHORT TITLE**

22 Northern Gannet rafting behaviour

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24 **KEY WORDS**

25 Habitat Use · Seabirds · Social Information · Special Protection Area · Celtic Sea

SUMMARY

- **Capsule:** Three quarters of tracked Northern Gannets (*Morus bassanus*) at Grassholm Island gathered in rafts around the colony, concentrated within a recently designated Special Protection Area (SPA) extension, but rafting was not correlated with foraging effort.

- **Aims:** To investigate the incidence, distribution and foraging implications of Northern Gannet rafting behaviour in waters adjacent to a large colony.

- **Methods:** Using bird-borne GPS we reconstructed at-sea behaviour and used a speed filter to identify rafting behaviour within 10 km of the colony. We mapped the spatial distribution of rafting events from 160 breeding individuals over 5 years, and investigated the relationship between foraging effort (trip duration and total distance travelled) and the presence/absence of rafting.

- **Results:** On average, 74% of tracked birds engaged in rafting. Of the 381 foraging trips analysed, rafting was recorded on 237 (62%). Birds were more likely to raft on outbound journeys (224 trips, 59%), than inbound (38 trips, 10%), however presence/absence of rafting did not correlate significantly with foraging trip length. The majority of rafting was concentrated in a 2-km radius around the colony within a recently designated seaward SPA extension. Birds show low repeatability in rafting, although there was lower variation within than among individuals.

- **Conclusion:** Our results suggest that rafting around the island is common among breeding gannets on Grassholm. A recent seaward SPA extension encapsulates the core distribution of rafting behaviour at this site. Rafting did not appear to be directly correlated with foraging behaviour. Given the dearth of literature on rafting and the wealth of GPS tracking data for seabirds, we suggest that similar research be conducted elsewhere to further elucidate the ecological significance of this behaviour and advise conservation management.

INTRODUCTION

Much applied and theoretical seabird research has focussed on the behaviour of birds attending breeding colonies (Bayer, 1982; Clode, 1993; Chaurand & Weimerskirch, 1994; Danchin & Wagner, 1997), and more recently miniaturised bio-logging devices have enabled the study of fine-scale distribution and behaviour while birds search for food at sea or visit wintering grounds (Weimerskirch, 2007; Burger & Shaffer, 2008; Wakefield *et al.*, 2009, 2013). However, relatively few studies have investigated how seabirds use waters adjacent to the colony, despite observations suggesting that many populations use such areas frequently (Burger, 1997; McSorley *et al.*, 2003).

Rafting appears to be important around seabird colonies for a number of reasons. Firstly, birds congregate on the water to engage in preening and bathing (Burger, 1997; McSorley *et al.*, 2003). These behaviours may be especially important for colonial seabirds because incubation and brooding periods can last weeks (Coulson, 2002) and high population density may lead to extensive plumage fouling from guano. Secondly, rafts may also provide an important source of social information. This information may be significant for locating a mate (Daniels *et al.*, 1994), for making decisions about where to recruit (Halley *et al.*, 1995), or may be related to foraging behaviour (Weimerskirch *et al.*, 2010; Racine *et al.*, 2012; Votier *et al.*, 2013; Machovsky-Capuska *et al.*, 2014; Thiebault *et al.*, 2014; Evans *et al.*, 2015). For example, Weimerskirch *et al.*, (2010) discovered that Guanay Cormorants (*Phalacrocorax* bougainvillii) use 'compass rafts' around the colony to signal the bearing of food patches to departing conspecifics and Machovsky-Capuska *et al.*, (2014) found evidence to support this hypothesis in Australasian Gannets (*Morus serrator*). With this in mind, investigating rafting at seabird colonies may yield further important discoveries for the study of seabird habitat use and foraging ecology, and may also have implications for conservation.

80   The present study utilises a large, fine-scale GPS tracking dataset of the at-sea movements

81   and behaviour of Northern Gannets (*Morus bassanus,* hereinafter 'gannet') to study rafting

82   behaviour in waters around a very large breeding colony at Grassholm, Wales. We employ a

83   speed filter to identify rafting and use this to (1) examine the incidence of rafting behaviour

84   for 389 foraging trips from 160 birds across 5 years and test for differences between the

85   sexes, (2) test the consistency (repeatability) of the rafting behaviour of individual birds, (3)

86   map the spatial distribution of rafting events within a 10-km radius of the colony to check the

87   effectiveness of a recent seaward extension of the Grassholm Special Protection Area (SPA)

88   at encompassing areas important for rafting, and (4) test the hypothesis that rafting is

89   correlated with foraging effort. Finally, we provide future directions for the role of rafting in

90   seabird research and conservation.

91

MATERIALS & METHODS

Study colony and bird sampling

94   Field work was conducted on Grassholm Island, Wales, UK (51° 43'N, 5° 28'W; Fig. 1)

95   during June and July in 2006 and, 2010-13. Approximately 40,000 pairs of gannets breed on

96   the island from April to October alongside several thousand immature and sub-adult non-

97   breeding birds. The island has been an SPA under EU law since 1986, and in October 2014

98   the Welsh Government approved a 2-km marine extension to account for aggregations of

99   birds using adjacent waters. Although daytime boat-based surveys of gannet activity in this

100 area have been conducted by the Joint Nature Conservation Committee (JNCC) (McSorley

101 *et al.*, 2003), no formal assessment of this behaviour had previously been published in the

102 peer-reviewed literature.

103

104 Chick-rearing gannets were caught using a brass noose or metal crook at the end of a

105 carbon-fibre pole under license from Natural Resources Wales (NRW) and the British Trust

106 for Ornithology (BTO). For sexing based on sex-linked genes, a blood sample (approx. 0.2

107 ml) was extracted from the tarsal vein under license from the UK Home Office and birds

sexed using standard techniques (AvianBiotech.com). Birds were caught on changeover (the point where brooding duties are switched) to minimise time that chicks were left unattended and to ensure that foraging trips began directly after release. Individuals were selected opportunistically within the periphery of the colony and fitted with a GPS logger and, for a sub-sample in 2010-2013, a time-depth recorder (TDR; see below). Birds were recaptured within 4-10 days to recover archival tags. Handling time was kept to a maximum of 15 minutes. All birds flew off strongly after release and showed no signs of immediate adverse effects.

Instrumentation

All birds (n=203; Table 1) were fitted with GPS loggers, secured to the base of the tail or back feathers using Tesa® tape. In 2006, ~65 g loggers from Earth & Ocean Technologies were used, but during 2010-11 the lighter (~30 g) i-gotU GT-600 loggers from MobileAction Technology were deployed, both programmed to obtain a fix every two minutes. During 2012-13 the further lighter (~20 g) i-gotU GT-120 GPS loggers were used and set to obtain a fix every minute. TDRs (G5; Cefas Technology Limited; 5.7 g; n=43) and LAT 1810 (Lotek Wireless Inc.; 10.5 g; n=26) devices were deployed, in combination with GPS loggers, on the underside of the central tail feathers during July 2010-13. The G5 TDR logged pressure and temperature every 0.1 seconds (10 Hz) during dives, and LOTEK LAT1810 TDR continuously at 1 second intervals (1 Hz).

Data screening

GPS tracking data were manually edited to focus on individual foraging tracks, removing fixes obtained while birds were stationary on the nest. Location fixes were interpolated using a cubic spline to a constant time interval of 60 seconds (Tremblay *et al.*, 2006), to avoid bias caused by mixed device duty cycles (see Appendix I). In some instances, the GPS logger battery expired before the completion of a foraging trip. For the purposes of this study, only complete trips from sexed birds were included (n=389 foraging trips from 160 individuals;

136   Table 1). Total trip duration and distance were calculated for each foraging trip. To filter out

137   GPS fixes of birds on the colony and to account for inherent positional error in GPS

138   transmissions, a minimum convex polygon was mapped around the island and data

139   intersecting this area were excluded (Fig. 1 inset map).

140

141   **Identifying rafting**

142   Rafting was defined as >1 consecutive GPS fixes below a speed threshold of 10 km h^{-1}. The

143   speed threshold was based upon visual inspection of a density plot of gannet travel speed

144   during foraging trips (Fig. 2) and is consistent with studies of flight speeds in the closely

145   related Cape Gannet (*Morus capensis*; Grémillet *et al.*, 2004). Circling behaviour may

146   produce artificially low groundspeed estimates, consequently, only sequences of GPS fixes

147   were counted as rafting events, removing single low-speed fixes. To test the sensitivity of the

148   screening regime, the analysis was repeated with >2 consecutive fixes (see Appendix II).

149   The resulting tracks, classified as rafting, show a directional pattern of close successive

150   fixes, consistent with contemporaneous tidal movement or wind vectors, indicating that the

151   behaviour captured is indeed most likely to represent birds resting on the water (Fig. 3).

152   Amélineau *et al.*, (2014) have shown that gannet movements <10 km h^{-1} may be related to

153   foraging, and so to check that slow movements of birds in this area were not caused by

154   foraging we analysed gannet dive data from 69 individuals on 117 foraging trips in July

155   2010-13 (for management of dive data see Appendix III). Distance from the colony was

156   calculated for each dive (n=2937) and plotted in a histogram (Fig. 4c). 0.51% (n=15) of

157   recorded dives were within 10 km of the colony, confirming that slow-moving birds in this

158   area are unlikely to be foraging (Fig 4b).

159

160   **Rafting study area**

161   To investigate rafting behaviour on waters around the colony, we focussed on an area with a

162   10-km radius from the centre of the island (51° 43' 51"N, 5° 28' 47"W; Fig. 1). This radius

163   was selected for two reasons. Firstly, while some birds may rest on the water outside this

164   area, we are specifically interested in rafting behaviour close to the colony. Secondly, casual

165   field observations and an initial qualitative assessment of tracking data indicate that rafting

166   tends to be concentrated in this area. Moreover, rafting appears to be found in a more

167   dispersed manner away from the colony, making it difficult to differentiate from foraging and

168   potentially concomitant during this behaviour (see Appendix IV).

169

170   **Data analysis**

171   GPS data were analysed per foraging track and rafting was separated into outbound or

172   inbound (pre/post foraging). Trips where birds left the colony to overnight on the water within

173   10 km of the island (n=8) were included in incidence and spatial distribution analyses but

174   excluded from analyses relating to foraging effort as they were unlikely to represent foraging

175   trips.

176

177   **1. Incidence**

178   We investigated the incidence of rafting using χ^2 contingency tables. First, we compared the

179   number of birds that rafted for each sampling year. Second, we determined whether the total

180   number of rafting birds was significantly different from those birds that did not raft. This

181   analysis was conducted for all birds combined and then compared between the sexes. Third,

182   we tested whether the number of outbound journeys that featured rafting events was

183   significantly different to that of inbound journeys. To investigate diel patterns in rafting, we

184   compared the time of day of foraging trip departures and of rafting events.

185

186   It is possible that birds may engage in extra bathing in response to handling for tag

187   application, which could be incorrectly interpreted as rafting. We therefore tested this by

188   comparing the frequency of birds that rafted outbound on the first foraging trip (i.e.

189   immediately after handling) with the frequency of birds that rafted during a second foraging

190   trip (i.e. several days after handling). Of the 160 birds included in the study, 150 recorded

191   complete trips immediately after handling, and 66 of these recorded a second trip.

2. Spatial distribution

A kernel density estimate (KDE) of the rafting fixes was created using a cell size of 10 m and a smoothing parameter (*h*) of 645 m in ArcMap™ 10.1. This produced a satisfactory bandwidth that would account for any positional error in GPS fixes, whilst other algorithms such as least squares cross validation (LSCV) were found to over-estimate range. 95% kernel cores were mapped for males and females separately to show the distribution of rafts for each sex. 25% contours were mapped for all rafting fixes. These were favoured over 50% contours for core habitat use to reduce the risk of a prolonged rafting event from one bird being counted as core habitat use at population level. We also calculated the number of rafting fixes located within the 2-km seaward SPA extension.

We calculated the distance from the centre of the colony for each rafting fix of males and females, and compared them in a two sample t-test to investigate differences in mean rafting range of males and females. Lastly we used contingency tables to determine whether there were any sex-specific or inter-annual differences in the use of the SPA.

3. Repeatability

To determine whether there were any consistent inter-individual differences in presence/absence of rafting behaviour, we calculated repeatability (r) using the R package 'rptR' (Nakagawa & Schielzeth, 2010). This approach tests the null hypothesis that between-individual variance equals within-individual variance in a binomial model. Only birds with repeat foraging trips were included in the analysis (n=74 individuals, 303 trips).

4. Rafting and foraging effort

Trip duration and total distance were used as metrics of foraging effort. These variables were found to be collinear (Spearman's Rank Correlation, r=0.92, n=381, p<0.001) and so were modelled separately to avoid the risk of a type II error (Zuur *et al.*, 2010). In all models,

220   sex and its two-way interaction was included as an explanatory covariate, and individual was

221   included as a random effect to account for pseudoreplication. To test the hypothesis that

222   rafting upon leaving the colony (hereinafter 'outbound') drives differences in (1) trip duration

223   and (2) total distance, we used Linear Mixed-Effects Models (LMMs). Response variables

224   were log-transformed to better approximate a normal distribution. To test the hypothesis that

225   differences in (1) trip duration and (2) total distance drive rafting upon return to the colony

226   (hereinafter 'inbound'), we used Generalized Linear Mixed-Effects Model (GLMM) logistic

227   regressions. GLMMs with 'binomial' error structure were required due to the binary response

228   variable (presence/absence of rafting). All analyses were undertaken using R 3.0.2 (R Core

229   Team, 2015) using the package 'lme4' (Bates *et al.*, 2014).

230

231   **RESULTS**

232   **Incidence**

233   The number of tracked gannets that engaged in rafting was significantly higher than those

234   that did not (74%; Table 2; χ^2_1=23.04, *p*<0.001). There was no significant difference in the

235   probability of rafting between males (73%) and females (64%) (Table 2; χ^2_1=0.591, *p*=0.442).

236   The incidence of rafting varied significantly among years (Table 2; χ^2_4=11.205, *p*=0.024) –

237   the lowest number of rafting birds was in 2013 (60%) and the highest in 2010 (100%).

238   Gannets were significantly more likely to raft outbound (59% of foraging trips, n=224) than

239   inbound (10% of foraging trips, n=38) (Table 3; χ^2_1=34.797, *p*<0.001). 14% of birds (n=21)

240   rafted both outbound and inbound on the same foraging trip (7% of foraging trips, n=25).

241   Overall, rafting was detected on 62% of foraging trips (n=237).

242

243   There was a clear diel pattern to foraging trip departures (χ^2_{23}=229.879, *p*<0.001), with 97%

244   between 06:00 and 21:00 (Fig. 5). Rafting events on foraging trips (n=273) followed a similar

245   diel pattern (χ^2_{23}=199, *p*<0.001) with 97% initiated between 06:00 and 21:00 (Fig. 5). Earliest

246   rafting initiated was at 02:50 inbound from a foraging trip, whilst the latest was at 23:34 also

9

247 on an inbound trip. Mean raft initiation was at 12:21 ± 241 mins. There was no significant

248 difference in rafting probability for birds on outbound trips immediately following handling

249 (58%) compared with those birds on trip 2 with no handling (52%) (χ^2_1=0.327, p=0.567).

250

251 **Spatial distribution**

252 Utilization distribution of rafting in the 10-km radius study area is indicated in Fig. 6. Although

253 mean rafting range was 3.8 ± 3 km, maximum extent of core habitat use (25% kernel cores)

254 at the population level was 2 km from the centre of the colony (Fig. 6). In sex-specific

255 analysis, mean rafting range for females (2.1 ± 1.9 km) was significantly smaller than for

256 males (4.4 ± 3.1 km; two sample t-test, $t_{3,443}$=30.663, p<0.001).

257

258 The extended SPA boundary (17 km^2) accounts for 5.4% of the total study area (314 km^2).

259 Of all rafting GPS fixes in the study area (n=4556), 46% were found to be within the

260 extended SPA boundary (Table 2). 91% of all rafting birds used this area. There was no

261 significant difference in the use of this area by rafting males (89%) compared with rafting

262 females (92%; Table 2; χ^2_1=0.05, p=0.824), and no significant inter-annual variation in the

263 proportion of rafting birds that used the area (Table 2; χ^2_4=4.44, p=0.35).

264

265 **Repeatability**

266 Individual birds showed low repeatability in the incidence of rafting behaviour, although there

267 was statistically lower variation within than among individuals (r=0.105 ± 0.05, p=0.001).

268 Both sexes showed low repeatability; males (r=0.156 ± 0.08, p=0.001) and females (r=0.034

269 ± 0.05, p=0.021), however males were significantly more repeatable than females

270 (χ^2_1=7.834, p=0.005).

271

272 **Rafting and foraging effort**

273   Mean foraging trip distance was 407.9 ± 275.4 km and mean trip duration was 1333 ±

274   1020.5 mins (Table 3). Rafting outbound was not significantly correlated with foraging trip

275   distance (Table 4; Fig. 7a; χ^2_1=0.464, p=0.496), with no significant sex effect (Table 4;

276   χ^2_1=2.032, p=0.154), and no significant interaction between rafting and sex (Table 4;

277   χ^2_1=1.02, p=0.31). Rafting outbound was not significantly correlated with trip duration (Table

278   4; Fig. 7b; χ^2_1=0.62, p=0.431). There was no significant sex effect (Table 4; χ^2_1=2.347,

279   p=0.126), and there was no significant interaction between sex and rafting (Table 4;

280   χ^2_1=0.612, p=0.434).

281

282   Propensity to raft inbound was not significantly correlated with foraging trip duration (Table 4;

283   Fig. 8a; χ^2_1=0.064, p=0.801), with no significant sex effect (Table 4; χ^2_1=0.606, p=0.437),

284   and no significant interaction between trip duration and sex (Table 4; χ^2_1=1.932, p=0.165).

285   Propensity to raft inbound was not significantly correlated with foraging trip distance (Table

286   4; Fig. 8b; χ^2_1=0.584, p=0.445), with no significant sex effect (Table 4; χ^2_1=0.573, p=0.449),

287   and no significant interaction between trip distance and sex (Table 4; χ^2_1=1.754, p=0.185).

288

289   **DISCUSSION**

290   Observations of seabird habitat use at colonies often describe aggregations of rafting birds

291   on adjacent waters (Burger, 1997; Weimerskirch *et al.*, 2010; Racine *et al.*, 2012). This study

292   supports these observations, showing that a high proportion (74% of tracked birds over 5

293   years) of studied gannets raft within 10 km of Grassholm, and that rafting is likely to occur on

294   over half (62%) of foraging trips undertaken by breeding birds. Spatial analysis shows that,

295   within the 10-km radius study site, rafting was concentrated within a 2-km radius of the

296   island (Fig. 6). Despite gannets showing sexual segregation of foraging habitat (Stauss *et*

297   *al.*, 2012; Cleasby *et al.*, 2015), sex appears to have little influence on the spatial distribution

298   of rafting; females recorded a smaller rafting range than males, however, ranges overlapped

299   and there was no significant sex difference in rafting propensity.

301 The waters immediately to the west of the island were found to be of particular importance

302 for rafting (Fig. 6). This is likely to be because the majority of breeding gannets as well as

303 large numbers of non-breeders are generally located here and this is the primary direction of

304 departure (Votier *et al.*, 2011). Our analysis of gannet dive data has shown that foraging is

305 not likely to occur in waters adjacent to the colony (Fig. 4), and therefore rafting in this area

306 is not concomitant with foraging and must have some other ecological significance.

307

Drivers of variation

309 Rafting behaviour has been poorly documented in most seabirds but recent studies have

310 shown that it may influence the foraging decisions of certain species; e.g. signalling the flight

311 bearing of food patches to conspecifics (Weimerskirch *et al.*, 2010; Machovsky-Capuska *et*

312 *al.*, 2014). Northern Gannets, however, appear to rely on personal memory to find prey,

313 showing high repeatability in foraging locations and departure angles (Pettex *et al.*, 2010,

314 2012; Patrick *et al.*, 2014; Waggitt *et al.*, 2014). Nevertheless, evidence is also emerging that

315 gannets use colonies as social information centres (Grémillet *et al.*, 2004; Votier *et al.*, 2013;

316 Wakefield *et al.*, 2013; Thiebault *et al.*, 2014) implying that the interplay between personal

317 and social information use remains poorly understood. A recent analysis of sub-colony

318 variation in foraging behaviour suggests that information transfer does not occur on the

319 colony itself (Waggitt *et al.*, 2014). Our analysis suggests that rafting is unlikely to be related

320 to these social information processes; we found that rafting outbound on foraging trips did

321 not drive variation in trip duration or total distance, although 85% of rafting events were

322 initiated on outbound journeys. Similarly, variation in trip duration and total distance did not

323 affect the propensity of birds to raft inbound. Therefore the preference of birds to raft

324 outbound could be motivated by a need to preen and clean soiled feathers after sitting on

325 the nest; plumage maintenance is likely to be essential to a bird's ability to fly and forage

326 effectively (e.g. for waterproofing), and to obtain a mate (e.g. appearing fit). Investigating the

327   potential relationship between the duration of nest attendance and propensity to raft

328   outbound could help to elucidate this in future studies.

329

330   Gannets show consistent individual differences in foraging behaviour (Votier *et al.*, 2010;

331   Patrick *et al.*, 2014, 2015; Wakefield *et al.*, 2015). Although gannets showed low

332   repeatability in rafting, the variance in this behaviour was significantly lower within than

333   between individuals. Moreover, while males were more repeatable than females, we do not

334   understand the reasons for this difference. The temporal distribution of rafting events follows

335   the temporal patterns expressed in foraging departures, and there was a strong diel pattern

336   to both (Fig. 6). This is largely attributed to the majority of rafting events occurring on

337   outbound journeys. There is a bias towards our capture of birds during daylight hours,

338   although gannets are thought to be inactive at night (Garthe *et al.*, 2003). We found

339   significant inter-annual variation in the incidence of rafting (Table 2). This suggests that

340   variation in the propensity of birds to raft could be driven by environmental factors at the

341   colony, or changes to prey distribution and abundance which may affect time budgets.

342   Moreover, weather conditions may affect a bird's necessity to clean its plumage, affecting

343   rafting propensity upon leaving the nest. Further investigation of wind, temperature and tidal

344   conditions at the colony and across foraging zones is required to explore this.

345

346   **SPA extension**

347 Seabirds face multiple threats both at sea and on land (Furness, 2003; Votier *et al.*, 2005;

348 Croxall *et al.*, 2012). European Union (EU), member states are required to designate the

349 'most suitable territories in number and size' for rare, vulnerable and migratory species as

350 SPAs under the European Commission's Directive on the Conservation of Wild Birds

351 (2009/147/EC). Although the majority of SPAs protect terrestrial habitat, the directive also

352 obliges member states to identify and protect important areas for aggregations of birds at

353 sea. Marine extensions to existing SPAs are implemented in the UK to fulfil this requirement

354 (McSorley *et al.*, 2003). Wilson *et al.* (2009) demonstrated that quantifying rafting activity

13

355   around colonies is effective in advising the implementation of such extensions to SPA

356   boundaries. Furthermore, given that rafting may be important for social processes and

357   ultimately population health, the argument for extending SPAs to encompass this behaviour

358   is growing. Grassholm SPA is a key nesting site for gannets, holding at least 12.5% of the

359   North Atlantic breeding population (Stroud *et al.*, 2001). Previously, the Grassholm SPA

360   covered the land to the mean low water mark, however, a 2-km seaward extension to

361   account for behaviour such as preening, bathing and displaying was recently approved. Here

362   we have shown that this area is used by 91% of rafting birds, and, although only

363   representing 5.4% of the 10-km radius study area, it encompasses 46% of all recorded

364   rafting activity. We therefore conclude that the SPA extension is effective in encompassing

365   rafting activity. Qualitative assessment of the data suggests that rafting events are likely to

366   be initiated in this area, with some birds then drifting away from the colony with tidal flow.

367

368   **Future directions**

369   The few studies of seabird rafting around the colony have employed either radio telemetry

370   (Wilson *et al.*, 2009) or observational data (Weimerskirch *et al.*, 2010; Machovsky-Capuska

371   *et al.*, 2014) to describe this behaviour. While these methods have improved our

372   understanding of rafting, they have a number of limitations. They are not only constrained by

373   the requirement of an observer at the colony but are associated with large errors and

374   restricted ranges. Conversely, biologging can reveal animal movement patterns with few

375   spatiotemporal limitations and a high degree of precision, including speed estimations

376   (Hooker *et al.*, 2007). Our study demonstrates that GPS loggers (as well as TDRs) are an

377   effective tool for identifying and quantifying rafting behaviour. Given the wealth of biologging

378   data for seabirds (Ropert-Coudert *et al.*, 2009), we suggest that similar studies would likely

379   improve our understanding of habitat use around the colony. This information could be used

380   to refine predictive models of seabird distribution and better advise the boundaries of future

381   SPA extensions (Grecian *et al.*, 2012). In order to further refine data screening, we propose

382   a number of considerations. Firstly, combining GPS tracking data with immersion data from

383   TDRs or geolocation sensors with saltwater switches could improve information on rafting.

384   For example, TDR data filtered to periods when the wet/dry sensor is activated, but the

385   pressure sensor does not indicate diving, could be combined with speed estimation to

386   remove doubt of any flight being mistaken as rafting. Secondly, this study is limited by the

387   temporal resolution of the data resulting from device duty cycles of >1 minute. Uncertainties

388   in bird behaviour could be elucidated by employing a finer scale resolution of one fix per

389   second for example. Moreover, observational data may offer greater insight into the function

390   of rafting by quantifying behaviour such as preening and bathing. Furthermore, including

391   tidal movements in the analysis would allow an evaluation of the accuracy of the screening

392   method. Quantifying tidal flow in the study area, and its variability, would help to determine a

393   more accurate speed threshold for birds resting on the water. Given that little is known about

394   rafting in most seabird species, combining biologging data with environmental data will no

395   doubt help to elucidate the ecological significance of this behaviour, and will likely have

396   positive outcomes for ecology and conservation.

397

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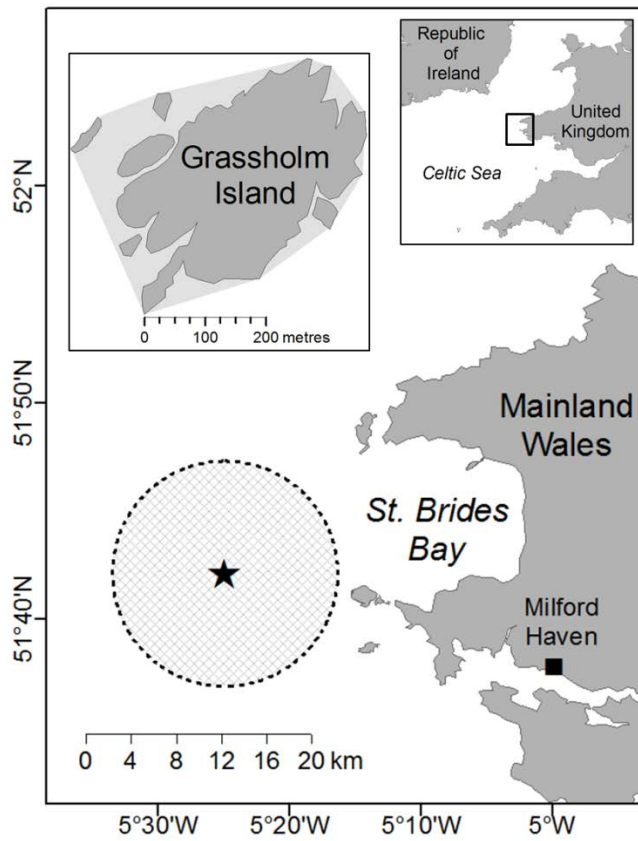
Fig. 1. Star indicates location of the study colony, Grassholm Island (51° 43'N, 5° 28'W), home to approximately 40,000 breeding pairs of Northern Gannets. Dashed line indicates the 10 km radius study limit (see "Rafting study area"). Inset map of the island indicates the minimum convex polygon (light grey area) defined around the colony to exclude GPS fixes of birds on the nest and to account for inherent positional error in GPS transmissions of birds on the island.
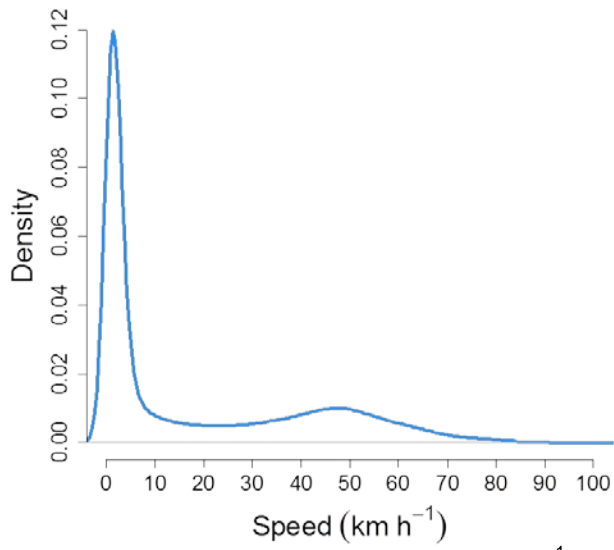
Fig. 2. Kernel density estimate of speed (km h^{-1}) for Northern Gannets. Data taken from all GPS fixes (n=511,572) during all complete tracks (n=389) and filtered to eliminate fixes of birds when stationary on nest. Kernel smoothing parameter (*h*) = 1.46.
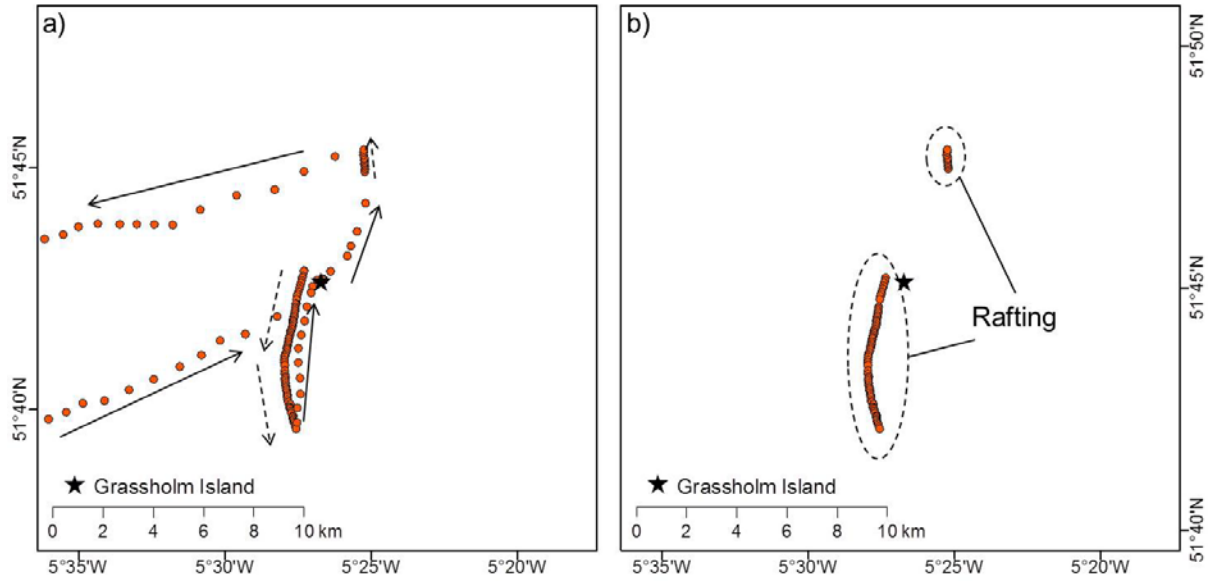
Fig. 3. GPS fixes for one gannet track (a) unfiltered and (b) filtered indicating that rafting events are qualitatively identifiable by directional patterns of close successive fixes. Arrows indicate direction of movement. Dashed arrows indicate movement <10 km h^{-1}.
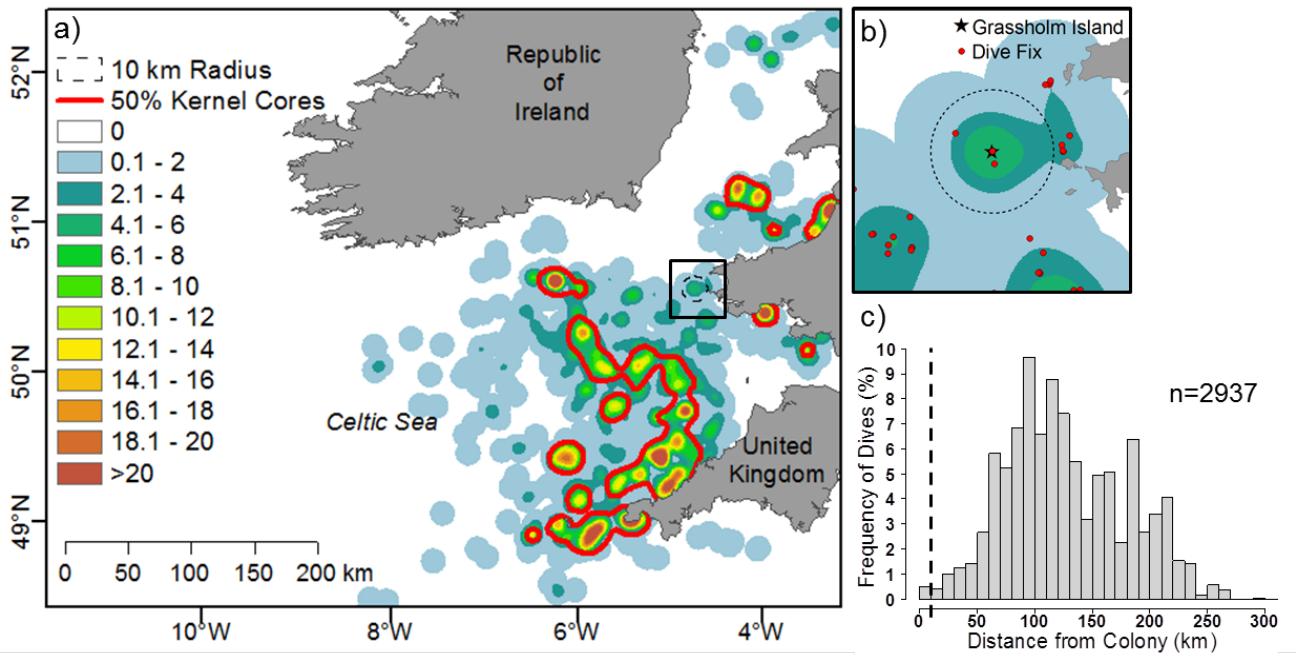
Fig. 4. (a) Kernel density estimate of dive fixes (n=2937) from 69 individuals on 117 foraging trips. Kernel smoothing parameter (*h*) = 10 km, cell size = 200 m. 50% kernel cores show core foraging areas. Colour palette indicates number of dive fixes per unit area. (b) Inset map shows close-up of the 10 km radius study area. (c) Percentage frequency histogram shows distance from colony of dive fixes with dashed line indicating 10 km radius. Slow moving birds within the study area are not likely to be foraging due to low density of dives.
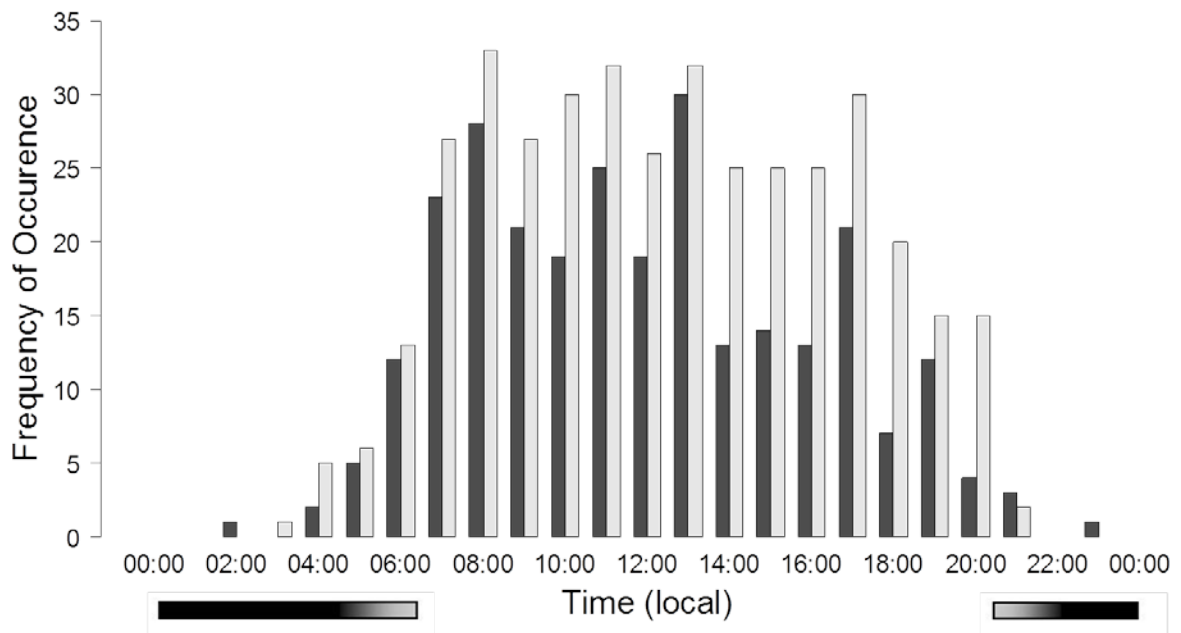
Fig. 5. Frequency distribution of time rafting events (n=262, dark bars) initiated, and departure times for foraging trips (n=389, light bars). Time shown in Greenwich Mean Time (GMT). Gradient bars on the x axis indicate hours of twilight and darkness.
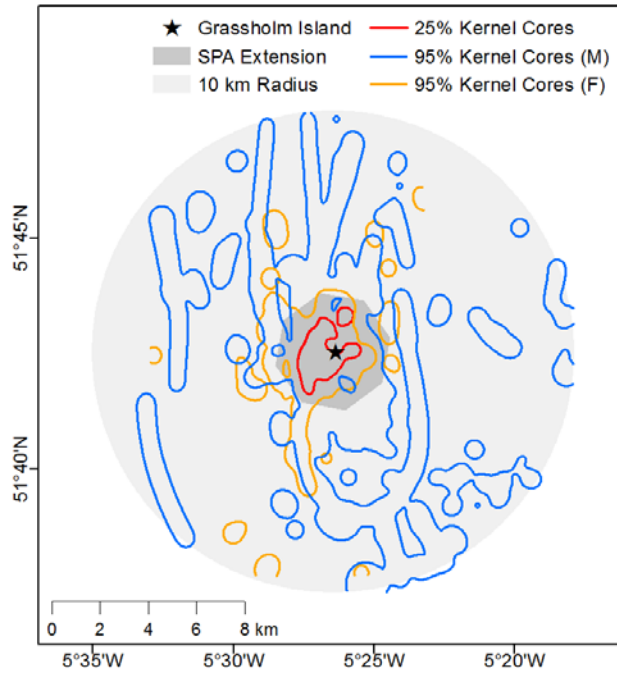
Fig. 6. Kernel density estimate of gannet rafting behaviour in a 10 km radius around the colony. 95% kernel cores represent majority of rafting within the study area for males (blue) and females (gold), 25% kernel cores represent core rafting areas for whole sampled population. Kernel smoothing parameter (*h*) = 645 m, cell size = 10 m. Dark grey polygon denotes recent 2 km radius seaward extension to SPA.
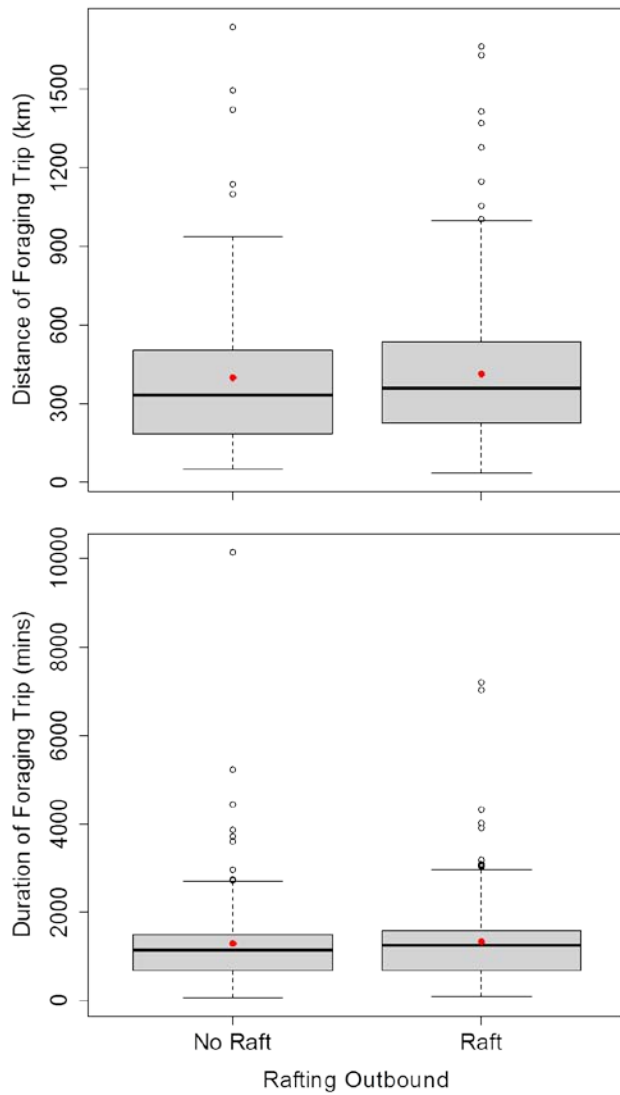
Fig. 7. Boxplots showing effect of presence/absence of outbound rafting on foraging trip (a) total distance (km) and (b) total duration (min). Thick black lines are median values, red dots are mean values, boxes show interquartile ranges, dotted lines show minimum and maximum values. Empty circles are outliers.
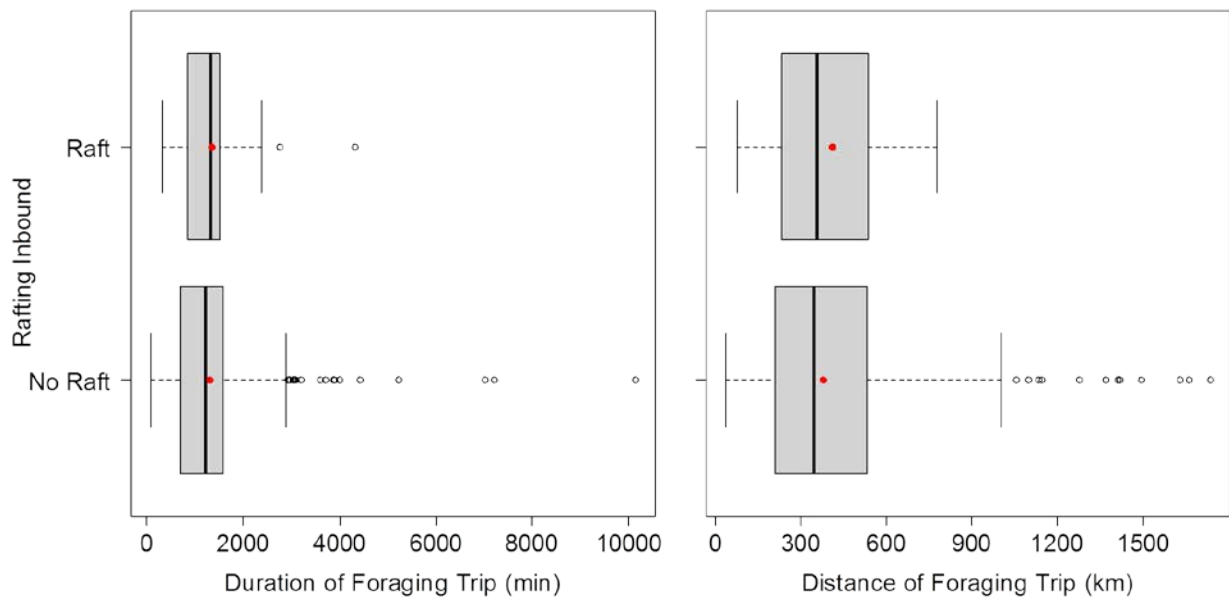
Fig. 8. Boxplots showing effect of foraging trip (a) total duration (min) and (b) total distance (km) on presence/absence of rafting inbound. Thick black lines are median values, red dots are mean values, boxes show interquartile ranges, dotted lines show minimum and maximum values. Empty circles are outliers.

TABLES

Table 1. Sample sizes of GPS tracked birds per year and the associated foraging trips included in this study. Only complete tracks from sexed birds were included for analysis here.

*Some foraging trips (n=8) were later found to be over-night rafting events with no foraging activity. These were included in spatial and incidence analysis of rafting but excluded from analysis of rafting and foraging effort.

	No. individuals tagged				No. individuals included			No. foraging trips included		
	Total	Male	Female	Sex Unknown	Total	Male	Female	Total	Male	Female
2006	26	15	11	0	22	13	9	28	17	11
2010	26	14	4	8	18	14	4	65	47	18
2011	54	22	15	17	34	19	15	173	89	84
2012	43	20	21	2	41	20	21	49	28	21
2013	54	20	30	4	45	19	26	74	30	44
Total	203	91	81	31	160	85	75	389*	211	178

Table 2. Incidence of rafting. Number of rafting birds and rafting GPS fixes within 10 km study area per year. Number of rafting birds and rafting GPS fixes recorded in SPA extension boundary and percentage of 10 km radius values. SPA boundary accounts for 17 km^2, 5.4% of total study area (314 km^2).

	Rafting within 10 km radius (% of studied birds)				Rafting within SPA boundary (% of 10 km radius values)			
	Total birds	Males	Females	No. GPS fixes	Total birds	Males	Females	No. GPS fixes
2006	17 (77%)	11 (85%)	6 (67%)	1068	16 (94%)	10 (91%)	6 (100%)	504 (47%)
2010	18 (100%)	14 (100%)	4 (100%)	638	18 (100%)	14 (100%)	4 (100%)	371 (58%)
2011	28 (82%)	15 (79%)	13 (87%)	1280	28 (100%)	15 (100%)	13 (100%)	570 (45%)
2012	29 (71%)	13 (65%)	16 (76%)	756	24 (83%)	11 (85%)	13 (81%)	348 (46%)
2013	27 (60%)	13 (68%)	14 (54%)	814	21 (78%)	9 (69%)	12 (86%)	285 (35%)
Total	118 (74%)	66 (73%)	52 (64%)	4556	107 (91%)	59 (89%)	48 (92%)	2078 (46%)

Table 3. Foraging trip parameters of male and female gannets. Distance and duration values are shown as means ± SD. n=381 foraging trips.

	Males	Females	Total
Foraging trip distance (km)	389 ± 257.1	425.2 ± 296.1	407.9 ± 275.4
Foraging trip duration (min)	1233.4 ± 808	1449.3 ± 1214.6	1333 ± 1020.5
No. trips w/ rafting outbound (% of foraging trips)	116 (57%)	108 (61%)	224 (59%)
No. trips w/ rafting inbound (% of foraging trips)	28 (14%)	10 (6%)	38 (10%)

Table 4. Model outputs for analysis of rafting and foraging effort. For all analyses sex was included as fixed effect and individual was a random effect.

						Main effect		Sex effect		Interaction dep. variable * sex	
Figure	Model	Response variable	Dependent variable	Error structure	df	χ^2	p	χ^2	p	χ^2	p
7a	LMM	Foraging trip distance	Pres./abs. rafting outbound	-	1	0.464	0.496	2.032	0.154	1.02	0.31
7b	LMM	Foraging trip duration	Pres./abs. rafting outbound	-	1	0.62	0.431	2.347	0.126	0.612	0.434
8a	GLMM	Pres./abs. rafting inbound	Foraging trip duration	"Binomial"	1	0.064	0.801	0.606	0.437	1.932	0.165
8b	GLMM	Pres./abs. rafting inbound	Foraging trip distance	"Binomial"	1	0.584	0.445	0.573	0.449	1.754	0.185

Interpolation of location fixes

GPS loggers recorded gannet locations at differing duty cycles. For this reason, it was necessary to interpolate location fixes to a constant one minute interval to avoid processing data at varying resolutions under the same regime. This process was conducted using a cubic spline interpolation in MATLAB. Fig. A1 shows some examples of the output from this procedure.
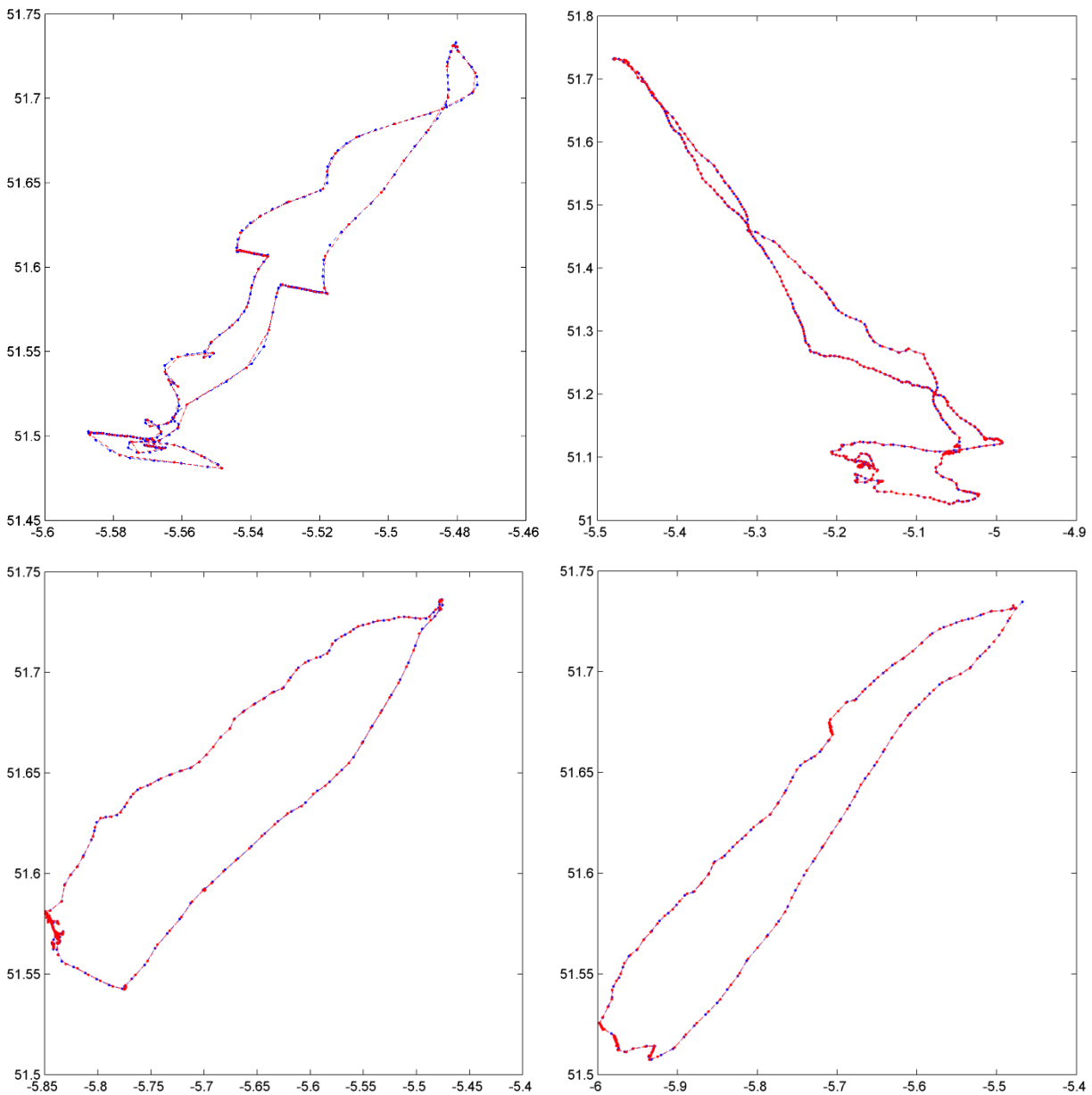

Fig. A1. Re-interpolation of GPS fixes for gannet foraging tracks. Red dots are original GPS fixes, blue dots are fixes re-interpolated to one minute intervals.

Sensitivity of methods

Data were screened to sequences of >1 consecutive GPS fixes to avoid counting low speed estimates generated by circling as rafting. To evaluate the sensitivity of this screening regime, we repeated the analysis with sequences >2 fixes. Comparing plotted fixes (Fig. A2a) and kernel density estimates (KDEs) (Fig. A2b) of both methods indicates that there is very little difference in the representation of the spatial distribution of rafting. The second method reports moderately less intensity of habitat use around the colony; 44% of fixes (n=1942) were recorded within the proposed SPA boundary; a negative difference of 2%. In the second analysis, however, 106 birds (66%) recorded rafting behaviour compared to 118 (74%) from the original analysis, although this difference is not significant (χ^2_1=0.457, p=0.499). This indicates that 12 birds included in the primary analysis recorded low-speed events of around 2 minutes. Although the second method recorded a lower incidence of rafting in the population, it is unlikely that this difference could be attributed to circling behaviour. Casual field observations of gannets circling at the colony suggest that this behaviour would be absorbed by data screening as they generally circle over the land.
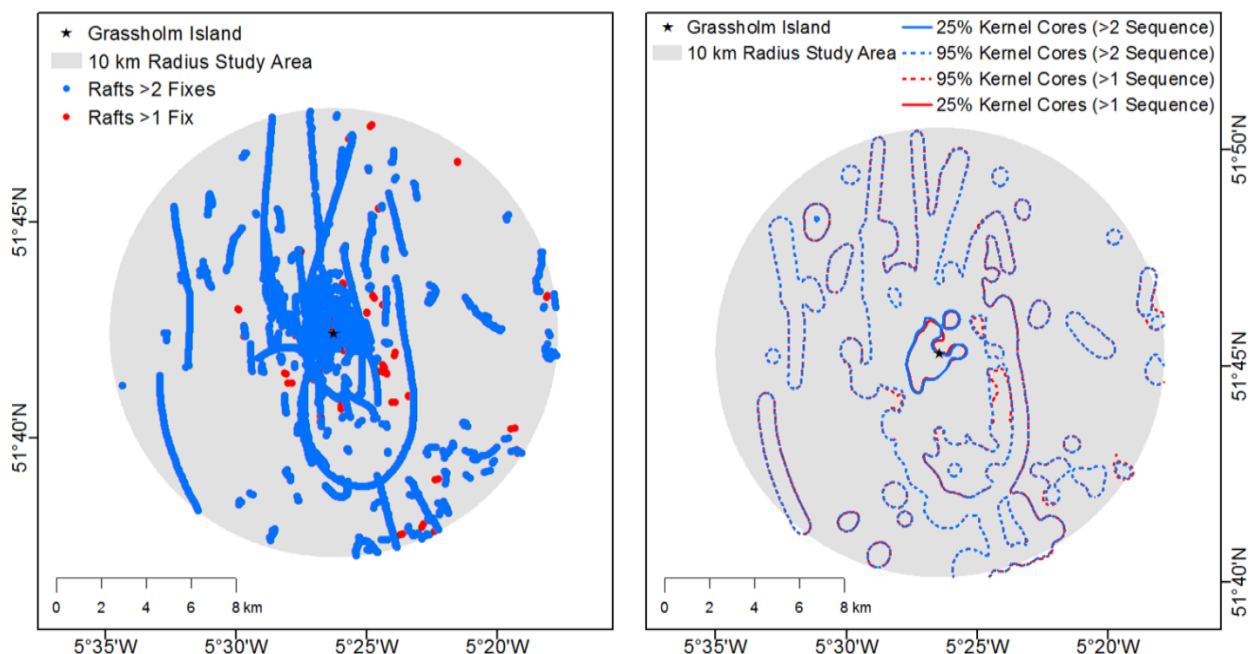

Fig. A2. (a) Plot of all rafting fixes in sequence >2 (blue) overlaid on fixes in sequence >1 (red). Visible red dots show rafting events that would be excluded with this method. (b) 95% isopleths

show rafting distribution for >2 sequence analysis (blue) overlaid on >1 sequence (red). Kernel smoothing parameter (*h*) = 645 m, cell size = 10 m. The isopleths show little variation in the way that the spatial distribution of rafting is represented.

APPENDIX III

Management of dive data

Dives, defined as periods when the pressure sensor of the TDR indicated activity at >1.5m depth, were matched to the closest GPS fix in time. Any dives occurring after the end of civil dusk (the point at which the centre of the sun is 6° below the local horizon) (n=<10) were deemed to be erroneous and were excluded from analysis, as gannets are known to be diurnal predators (Garthe *et al.*, 2003). A kernel density estimate (KDE) of dive fixes was mapped using a smoothing parameter (*h*) of 10 km and a cell size of 200 m (Fig. 4b). This smoothing parameter was selected in accordance with a previously documented mean scale of area restricted search (ARS) behaviour for this species (9.1 ± 1.9 km; Hamer *et al.,* 2009). 50% kernel cores were calculated to show core foraging range.
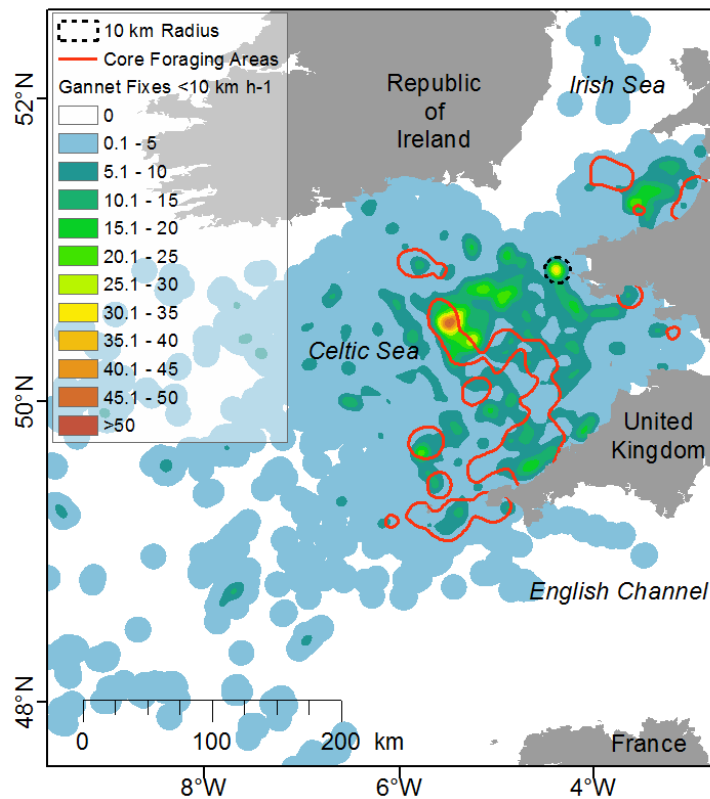
APPENDIX IV

Extent of rafting

Fig. A3. Kernel density estimate of GPS location fixes of birds travelling <10 km h^{-1} together with core foraging areas (red lines) calculated from 50% kernel cores of gannet dives (see Fig. 4b). Kernel smoothing parameter (h) = 10 km, cell size = 200 m. Colour palette indicates number of GPS fixes per unit area. This map shows that, although rafting is clustered around the colony, it appears to occur also on a wider scale. Rafting away from the colony may coincide with foraging.

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