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Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices

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2 **attachment of GPS and time-depth-recorder devices**

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4 **Running head**

5 Foraging behaviour of common murres

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13

14 **Abstract**

15 GPS and time-depth recorders were deployed in combination to investigate foraging

16 behaviour of common murres (*Uria aalge*) breeding at Stora Karlsö island, Baltic Sea during

17 the chick rearing period. In the pre-breeding period the main prey species sprat (*Sprattus

18 sprattus*) of murres is targeted by commercial fisheries, likely reducing prey availability

19 during the breeding season. Foraging trips typically consisted of a short flight followed by a

20 period sitting on the sea surface (0.39 ± 0.48 h), followed by several (5.3 ± 3.8) diving bouts

21 interspersed by flights and water surface activity. Following the final diving bout murres

22 returned directly to the colony. Overnight foraging trips lasted longer than daytime trips and

23 that corresponded with greater diving activity and reduced dive depths around dawn and

24 dusk, likely times of high prey accessibility. High outward flight groundspeeds (20.0 ± 2.8 ms⁻

25   [1]) are aided by tailwinds and lower inward flight groundspeeds (15.1 ± 2.5 ms^{-1}) impeded by

26   headwinds. Flights following the wind direction may reflect a strategy to reduce crosswind

27   drift. Foraging intensity was lower than reported by most other studies of murres suggesting

28   more abundant or aggregated prey.

29

30   **Keywords**

31   Foraging behaviour, diving behaviour, *Uria aalge*, common murre, wildlife telemetry, data

32   loggers, Baltic Sea

33

34 **Introduction**

35 To understand the breeding ecology and behaviour of seabirds it is necessary to study their

36 behaviour both at the breeding colony and at sea. At the colony, detailed visual

37 observations can be made, at sea visual observation can only provide brief snapshots of

38 behaviour and the individual colony of origin and the breeding status of individuals are

39 unknown (*e.g.* Scott 1990, Davoren et al. 2002). In recent years, the development of

40 miniaturised electronic devices has allowed recording of detailed behaviour at sea

41 (reviewed by Burger & Shaffer 2008). Studies on alcids were conducted with regard to both

42 spatial (*e.g.* Benvenuti et al. 1998, Thaxter et al. 2009) and diving behaviour (*e.g.* Tremblay

43 et al. 2003, Paredes et al. 2008). In this paper we describe how two commercially available

44 devices were used simultaneously to record both diving activity and spatial activity in a large

45 alcid, the common murre (*Uria aalge*).

46 As single prey loaders, chick-rearing adult murres return from foraging trips with one fish

47 held length-ways in the beak to feed to the chick (Bradstreet & Brown 1985), limiting

48 foraging range when chicks are fed several times a day. This may lead to local depletion of

49 fish populations near the colony and puts pressure on birds to travel further to forage at

50 larger colonies, termed 'Storer-Ashmole's halo' (Ashmole 1963 reviewed in Elliott et al.

51 2009a, Gaston et al. 2007). By combining GPS and time-depth recorder (TDR) devices it is

52 possible to determine the positions of final diving bouts, *i.e.* where the prey is captured for a

53 chick.

54 In the Baltic Sea, a large-scale shift has occurred from a cod (*Gadus morhua*) dominated to

55 sprat (*Sprattus sprattus*) dominated ecosystem. This may have occurred due to a

56 combination of anthropogenic drivers, such as fishing pressure and eutrophication, and

57   climate change with sprat numbers increasing following reduced predation by cod

58   (MacKenzie et al. 2002, Casini et al. 2009, 2011, Möllmann et al. 2009). Common murres in

59   the Baltic Sea are heavily dependent on sprat (Lyngs & Durinck 1998). Thus, this change in

60   the dominant species meant a strong increase in prey abundance, but also a reduction in

61   prey condition and weight, resulting in a reduction in prey quality (Österblom et al. 2006,

62   Casini et al. 2011). In recent years, when the cod fishery was reduced, cod numbers have

63   started to recover. At the same time fishing pressure on sprat has increased resulting in a

64   decrease in biomass of *c.* 30% since a peak in the late 1990s (ICES 2010). However, on the

65   scale of the Baltic Sea, sprat abundance is still high in comparison with the 1970s and 1980s

66   when numbers were at approximately one third of 2009 levels (ICES 2010). The sprat fishery

67   near Stora Karlsö practically ceases from June to August, so it is not in direct competition

68   with murres during the breeding season. However, if fish numbers are sufficiently depleted

69   by the beginning of the breeding season, murres may have high foraging effort, with rapid

70   depletion of fish close to the island. Alternatively, fish numbers are not reduced to low

71   levels, but as sprat disperse following spawning, requiring more effort to catch, a

72   commercial fishing operation may cease to be economically viable. If this reduced

73   aggregation influences the birds, we would expect murres to use a large area of sea to

74   forage. Anecdotal evidence (*e.g.* observations by fishermen) suggests that foraging murres

75   from the Karlsö islands use a wide area and concentrate off the northern tip of Öland and

76   south of Gotland at the Hoburgs Bank (Fig. 1).

77   In this paper we describe the foraging behaviour of chick rearing common murres using

78   simultaneous GPS device (GPSD) and TDR deployment. The study aimed to gain a broad

79   picture of foraging activity at Stora Karlsö, recording foraging locations, temporal patterns,

80   and foraging strategies. The detailed data allows a fine-scale analysis of activity during

81 foraging trips, as well as whether multiple foraging sites are used during a trip and the

82 behaviour at the start of a trip. The GPS data allow foraging flights to be analysed, including

83 how these may be affected by wind. We hypothesise that foraging routes and locations are

84 affected by wind speed and direction. We predict that foraging activity will be concentrated

85 around dusk and dawn, as has been found for several other locations (*e.g.* Regular *et al.*

86 2010). This population has relatively high reproductive output (*e.g.* fledging success 0.88 –

87 0.97 in years prior to study) and a stable or increasing population size (Kadin et al. 2012,

88 unpublished data) and therefore we expect that foraging and diving effort will be equivalent

89 or lower to other murre colonies. This is the first study describing the foraging strategies of

90 common murres in the Baltic Sea.

91

92 **Methods**

93 **Study site and species**

94 The study took place at Stora Karlsö island, Sweden (57˚17' N, 17˚58' E), in the south-

95 eastern Baltic Sea (Fig. 1). Some 8000 pairs (Österblom et al. 2002) of common murres (*Uria*

96 *aalge*, Pontoppidan 1763) breed here, somewhat more than the neighbouring island of Lilla

97 Karlsö (Lyngs 1993). Field work took place from the 9 - 20 June 2009; with devices deployed

98 from 9 - 15 June 2009. Common murres are present at the breeding colony during late

99 winter, with daily presence from mid-April, when the breeding period begins. Experienced

100 birds typically show both high site and mate fidelity (Moody *et al.* 2004). In mid-April mating

101 occurs, *c.* 15 d later a single egg is laid (Hatchwell & Pellatt 1990). After hatching, both

102 parents provision the chick (Kadin et al. 2012), with *c.* 3 - 5 feeds d^{-1} (Österblom & Olsson

103 2002, Thaxter et al. 2009). At 15 – 30 d the still flightless chick leaves the colony

104 accompanied by the male parent on whom it continues to depend on for over a month

105 (Scott 1990). Breeding adults were caught from the same natural rock ledge sited directly

106 beneath an artificial breeding cliff structure (described by Hentati-Sundberg et al. 2012). At

107 the base of this structure was a trapdoor in the floor, through which we caught the birds by

108 using a noose pole.

109 **Bird-borne data loggers**

110 We used two different devices together: a back-mounted GPSD (model GT-120 by Mobile

111 Action Technology, Inc. Taipei, Taiwan) and a leg-mounted TDR (model LAT 1500 by Lotek

112 Wireless, Ontario, Canada) to record the foraging movements and diving behaviour

113 (detailed description in S1 in the supplement at *****). Eight GPSD were deployed, half

114 were set to record every 90 s, the others every 60 s, all but two were set to turn off from

115 2300 h to 0300 h local time (time in CEST unless stated), to save power at a time when

116 activity was expected to be low (*e.g.* Regular et al. 2010). Two versions of the TDR were

117 used, either with 50 (n = 3) or 500 m (n = 8) depth limits. All GPSD deployments included a

118 TDR, but three TDR were deployed without a GPSD, resulting in eight GPSD with TDR

119 deployments, and three TDR only deployments. We attached an identification ring to the

120 right leg of the bird, following the Swedish Bird Ringing Centre scheme (Naturhistoriska

121 riksmuseet, Stockholm). The TDR was then mounted on an aluminium leg ring. With the GPS

122 attached to back feathers using several strips of black Tesa marine tape (product 4651 from

123 Tesa SE, Hamburg, Germany). Total weight of bird-borne instrumentation (including

124 identification ring, attachments and devices) was *c.* 29 g equivalent to *c.* 3 % (range 2.9 – 3.8

125 %) of body weight for the study birds.

126   Owing to some deployments with both GPSD and TDR and others with only TDR, it was

127   necessary to use different parts of the data-set depending on the analysis. Thus, sample

128   sizes differ depending on the factor of interest. We recovered devices from 7 common

129   murres tracked during the breeding period. Six of GPSD with TDR, and one TDR only; the

130   remaining four birds were not recaptured, so devices could not be recovered. However,

131   these birds were observed on the breeding-ledge apparently continuing chick provisioning.

132   There were three 60 s and three 90 s interval GPSDs. One 60 s and one 90 s devices failed

133   for unknown reasons after 4 and 12 h, respectively. The remaining 4 devices recorded on

134   average for 53 and 58 h for the 60 s and 90 s devices, respectively. In total 27 foraging trips

135   were tracked, of which 18 were complete, 22 included at least the start and end of the trips;

136   the remaining 5 missed the start or end positions (detailed sample sizes in S1).

137   **Data treatment and statistics**

138   TDR data were analysed in MultiTrace-Dive (Jensen Software Systems, Laboe, Germany) to

139   recognise and parameterize each dive and sequence of dives, *i.e.* a dive bout. An activity

140   was classified as a dive when having a maximum depth of at least 3 m (after Paredes et al.

141   2008); the start and end of a dive was set when 5 % of the maximum dive depth was

142   exceeded or reached, respectively. The bottom-phase of the dive, which roughly represents

143   the portion of the dive spent actively foraging, was defined as time >75 % maximum dive

144   depth (Tremblay et al. 2003, Halsey et al. 2007). We calculated various measures for each

145   dive, including dive duration, maximum dive depth, and vertical ascent and descent rates.

146   To investigate the minimal recovery period following dives, data were pooled, and minimum

147   post-dive interval (PDI) values taken for each dive duration at one second resolution was

148   plotted against dive duration (Fig. 8 A). Dive efficiency was calculated as (Camphuysen et al.

149   2005):

150 *Dive efficiency = bottom time / (dive duration + PDI)*

151 Dive bouts, "periods of sustained diving activity" (Thaxter et al. 2010), are a sequence of

152 dives with only brief PDI. Definitions of dive bouts differ, generally using either a fixed

153 criterion, or varying, for example using both differences in dive depths and PDI (*e.g.* Mori et

154 al. 2001). Here the method of Sibly et al. (1990) was applied to calculate a fixed maximum

155 PDI providing a bout ending criterion (Paredes et al. 2008, Hedd et al. 2009), plotting

156 log(frequency) against PDI using the R statistical environment (R Development Core Team

157 2010) with package 'HyperbolicDist' (Scott 2009). A natural cut-off indicating the end of a

158 bout was 250 s. Various measures were calculated for dive bouts, e.g. number of dives and

159 mean maximum dive depths.

160 We analysed foraging trips using a combination of GPSD and TDR data, which allowed trip

161 start and end times to be determined. We classified behaviour during trips into four

162 categories; (1) diving bouts, (2) splashdown, (3) surface resting, and (4) flight (see S1).

163 'Splashdown' periods were recognised as the first uninterrupted (*i.e.* with no flight or diving)

164 period of water surface activity (Burger 1997, Davoren et al. 2003).

165 Data from the GPSDs were mapped in ArcMap (9.3 and 10.0, Environmental Systems

166 Research Institute, Redlands, CA), with which all map figures were produced.

167 To compare the distance from the colony of final dive bouts, and the rest of dive bouts (non-

168 final dive bouts) occurring during each foraging trip, we calculated the ratio of the distance

169 from the breeding-ledge for a dive bout to the maximum distance reached during a trip. To

170 compare final bouts with non-final bouts, the mean ratio was calculated for non-final dive

171 bouts for each foraging trip, producing an index, allowing comparison irrespective of actual

172 distances. In a paired t-test these two values were compared with all foraging trips pooled.

173   To examine how trip duration relates to activity on foraging trips, we looked at, (1) the

174   maximum distance from the colony reached, (2) number of dives, and (3) the number of

175   bouts per a foraging trip. Although time of day is likely to affect activity (*e.g.* Fig. 5), this was

176   not included in our models because of the small sample size. We developed linear mixed-

177   effects models (LMMs) with individual as a random effect. Model selection and validation

178   followed that outlined by Zuur et al. (2009), using the 'nlme' package (Pinheiro et al. 2011)

179   in R.

180   Flight segments were separated from GPS data (see S1) to analyse flight activity. Amongst

181   other parameters we calculated ground speed, the speed of the bird relative to the ground,

182   as opposed to 'air speed', the speed travelled relative to the air mass. We classified flights

183   into three groups. (1) Outward flight included flights between breeding-ledge departure and

184   the first diving bout (this included the flight both before and after a splashdown). (2)

185   Foraging flights were any flights during a trip that occurred after the first dive bout and

186   before the final dive bout. (3) Inward flights took place from the final dive bout to arrival at

187   the breeding-ledge. Wind data from a nearby weather station (70 km from the study site at

188   the north point of the island of Öland, fig. 1) gave the median wind direction in 10° bins and

189   mean wind speed at 1 ms^{-1} resolution, both in 3 hour blocks.

190   We looked at possible device effects on the study birds, through weight change and

191   breeding success (in the supplement, S2, at ******).

192   Figures were generated and statistical analyses performed with R (R Development Core

193   Team 2010), except for the maps which were produced in ArcGIS. Some circular statistics

194   and figure 7 parts A, C and E were generated with Oriana (Kovach Computing Services,

195   Pentraeth, Anglesey, UK).

196

197   **Results**

198   **Foraging trips and time activity budget**

199   Foraging trips usually started with a short flight to a splash-down period, before the birds

200   either dived or flew to a foraging site then dived (see Fig. 2 and 3). Dives occurred in short

201   sequences, bouts, with short PDI. Several dive bouts occurred per trip sometimes with short

202   flights between these. After the final dive, birds usually flew directly to the breeding-ledge,

203   presumably to feed their chick although this was not systematically observed. This final dive

204   bout generally occurred close to the maximum distance from the breeding-ledge (Fig. 3 &

205   Fig. 6 D).

206   During foraging trips a high proportion of time was spent on the sea surface (>40 %), with

207   slightly less time actively foraging in dive bouts (<40 %). The remaining time (<20 %) (Table

208   1) was dedicated to flight. During dive bouts, approximately a quarter of the time was spent

209   recovering during PDIs. Trip durations were variable (Fig. 4 A), with a median value of 3.1 h,

210   somewhat less than the mean value (Table 1), suggesting many shorter trips with few much

211   longer trips. Trips with evening departures were typically longer in duration than daytime

212   trips (Fig. 5 A). Four out of five trips occurring after 1900 h were >6 h, and no trip >6 h

213   started between midnight and 1900 h. The longer the duration of a foraging trip, the greater

214   the maximum distance reached from the breeding colony (Fig. 6 A). This relationship did not

215   appear to differ among individuals. LMMs included individual as a random effect with

216   random intercept and slope or random intercept only both were less parsimonious (higher

217   AIC values).

218   Diving activity increased with trip duration, both the number of dives (Fig. 6 B), and the

219   number of dive bouts (Fig. 6 C). For both factors, the most parsimonious model did not

220   include individual (selected by AIC) suggesting that little variation was explained by

221   individual. Trip duration (Fig. 4 A) and the maximum distance from the breeding-ledge

222   reached during trips (Fig. 4 B) showed great variation, though distance was more uniform in

223   distribution. The total distance travelled (Table 1) was only slightly more than double the

224   maximum distance reached (mean ratio 2.26 ± 0.20), indicating that routes followed were

225   direct (Fig. 3), with straight flights too (Table 2).

226   **Flight behaviour**

227   Flights were of intermediate distance, being several km and generally <500 s (Table 2). Flight

228   ground speeds recorded by the GPSD were very variable ranging from *c.* 5 m s^{-1} up to 32 m s^{-1}

229   (Fig. S1 in supplementary material at *****), this reflecting (1) the variation in air-speed,

230   (2) wind conditions (Fig. 7 E & F), (3) or a combination of these. Outward flights mostly

231   occurred over a fairly narrow sector to the north-west of the island (Fig. 7 A). The mean

232   ground speed during outward flights was greater than during inward flights (Fig. 7 B, D),

233   with outward flights typically having a tailwind component and inward flight a headwind.

234   **Diving behaviour**

235   Dive depths followed a bimodal distribution (Fig. 8 C) but dive duration (Fig. 8 B) showed a

236   unimodal distribution. Dive parameters are summarised (Table 3). The majority of dives

237   were U shaped with a broadness index mostly >0.015 (the V-shape threshold; Halsey et al.

238   2007) (Fig. 8 D). Therefore, dive shapes were not analysed further. The minimum surface

239   recovery period, PDI value, increased with dive duration with a steep increase beyond 150 s

240   (Fig. 8 A). On average the dive time was slightly more than double the PDI (Table 3). Diving

241   frequency was greatest in the evening (Fig. 5 B), from 1700 h - 2300 h (local solar time), and

242   around dawn (0100 h – 0300 h). Mean dive depths were near constant from 0300 h - 2100

243   h, but then reduced from 2100 h – 0300 h reaching a minimum around midnight (Fig. 5 C).

244

Discussion

246   We found that most foraging parameters measured for common murres in the Baltic Sea

247   were similar to those recorded at other sites, but some findings indicated good foraging

248   conditions for breeding murres. Furthermore, the murres used a limited foraging area

249   suggesting that prey was aggregated rather than dispersed. Alternatively the wind

250   conditions may have influenced the use of foraging areas. However, our study period was

251   limited and thus may not be representative of the general conditions throughout the season

252   or between years. These detailed insights into foraging behaviour add to our understanding

253   of murre foraging. For example, the possible use of a bimodal foraging strategy, with long

254   overnight trips, and shorter daytime trips , a behaviour that would be less apparent in

255   studies relying on TDRs alone.

Splashdowns

257   Most foraging trips began with a splashdown period where birds landed on the water

258   surface close to the colony, a similar pattern to that of other studies of common and thick-

259   billed murres (Burger 1997, Elliott et al. 2009b). This suggests that splashdowns are

260   important, although their primary function is debated. It may offer the opportunity to clean

261   plumage (Elliott et al. 2009b), but may also play a role in determining foraging direction as

262   departing birds observe the direction of incoming birds (Burger 1997). A similar behaviour

263   has been observed in breeding colonies of Guanay cormorants (*Phalacrocorax bougainvillii*)

264   (Weimerskirch et al. 2010).

Foraging distance and duration

266   The duration and maximum distances of foraging trips observed at Stora Karlsö is

267   comparable to those measured in other studies (*e.g.* Tremblay et al. 2003, Thaxter et al.

268   2010), though trip duration was short in 2009 (Kadin et al. 2012). Stora Karlsö is a relatively

269   small colony compared to other sites, where tens of thousands of pairs are not uncommon,

270   thus competition may be relatively low. There may also be less intra-specific competition

271   compared to other colonies, with few large colonies nearby, although there may be inter-

272   specific competition with razorbills of which there are similar numbers to murres at Stora

273   Karlsö (Hedgren & Kolehmainen 2006) and with smaller populations on the neighbouring

274   island of Lilla Karlsö (Lyngs 1993).

275   **Flight behaviour and wind**

276   Murre foraging flights largely occurred on the same axis as winds, with outward flight with

277   tailwinds and inward flight into headwinds. This could represent a strategy to reduce

278   crosswind wind drift over the sea where a fixed frame of reference thought necessary to

279   assess drift is unavailable (Åkesson & Hedenström 2007). However partial compensation for

280   wind drift may be possible by: (1) Maintaining optical flow (the time taken for an object to

281   pass across the retina) by selecting flight altitude, as used by some insects over land and

282   water (Riley et al. 1999, Srygley & Dudley 2008). (2) Using the 'wave landscape', the pattern

283   of waves over the sea as a fixed reference which could allow for partial compensation as the

284   wave patterns would change slower than wind speeds (Alerstam & Pettersson 1976). (3)

285   Using coastline as a fixed reference (e.g. Åkesson 1993). Preferences for headwinds were

286   observed for alcids at sea (Spear & Ainley 1997), with their high airspeed associated with

287   high wing loading, avoidance of headwinds for energetic reasons may be reduced given

288   orientation advantages (drift avoidance) of avoiding crosswind conditions, though high wind

289   speeds have been shown to increase energy expenditure by auks (Furness & Bryant 1996).

290 **Dive activity**

291 The mean maximum dive depths of common murres at Stora Karlsö of 20 – 50 m were

292 similar to those recorded at other colonies (*e.g.* Camphuysen 2005, Hedd et al. 2009;

293 Thaxter et al. 2009). As were dive efficiency values (Hedd et al. 2009, Thaxter et al. 2010). A

294 steep increase in PDI for dive durations over 150 s adds support to the proposition of a

295 'behavioural aerobic dive limit' at this point for common murres (Tremblay et al. 2003, also

296 Fig. 4B in Thaxter et al. 2010) that was also found in thick-billed murres (Croll et al. 1992);

297 this may represent the actual aerobic dive limit (Hansen & Ricklefs 2004).

298 **Daily activity patterns**

299 We found a strong diel activity pattern, in agreement with many other studies of alcids and

300 of observational studies of chick provisioning at this colony (Österblom & Olsson 2002). Like

301 razorbills (*Alca torda*) in the southern Baltic Sea (Benvenuti et al. 2001), the common murres

302 at Stora Karlsö followed a bimodal foraging strategy with longer duration overnight trips and

303 shorter daytime trips. This pattern is likely to reflect the most profitable foraging times

304 (around dusk and dawn) when diving activity was greatest and diving depths were rather

305 shallow. This pattern was also found in several other studies for breeding (Camphuysen

306 2005, Regular et al. 2010) and post-breeding murres (Nevins 2004). This pattern probably

307 reflects a balance between prey being accessible near the water surface and the time when

308 sufficient light is available for visual foraging (Regular et al. 2010, Regular et al. 2011). The

309 primary prey species for murres at Stora Karlsö, sprat, is known to perform a diel migration

310 (Cardinale et al. 2003), moving to surface waters at night.

311 **Foraging conditions**

312 The use of longer trips in addition to short trips, radial pattern of trip paths, and the

313 presence of diving towards the most distant part of these trips supports the proposition that

314   prey closer to the colony could be depleted, favouring more distant foraging sites. However,

315   the use of a limited sector of the sea suggests prey may not be widely dispersed but

316   aggregated. However, this may also reflect a preference for flights in headwinds and

317   tailwinds (see above). Stora Karlsö murres performed slightly fewer dives per dive bout and

318   per foraging trip, suggesting higher prey availability. This may indicate little competition

319   between fisheries and murres in this part of the Baltic Sea in 2009. It may also explain the

320   stable or growing population at this breeding colony (Kadin et al. 2012) in contrast to other

321   colonies of the species, *e.g.* around the North (JNCC 2011) and Norwegian Seas (Barrett *et*

322   *al.* 2006) which have been decreasing in size. Further information about other sprat-

323   dependent species is necessary to fully understand interactions between seabirds and the

324   sprat fishery.

325   **Conclusions**

326   The combined use of separate GPS and TDR devices provides detailed behavioural data,

327   which contribute novel information on individual alcid foraging decisions. The foraging trips

328   for chick rearing common murre breeding at Stora Karlsö typically start with a short

329   splashdown period followed by several, often spatially separated diving bouts. These diving

330   bouts were interspersed with periods of surface activity and short flights. After the final

331   diving bout, which typically occurred at the greatest distance from the breeding colony,

332   birds usually returned directly to the breeding-ledge. During the study period, outward

333   flights were significantly faster than inward flights, probably due to tailwind assistance. The

334   murres appear to select either headwinds or tailwinds, avoiding crosswinds, and this may

335   affect foraging locations chosen. However, to confirm these observations, studies under

336   more variable wind conditions are required. There was a strong temporal pattern in foraging

337   activity, with an apparent bimodal foraging strategy of long overnight trips, and short

338   daytime trips. Diving frequency was greatest in the evening and dawn when diving depths

339   were least.The present study illustrates how detailed information about foraging behaviour

340   can be used to assess locations and activities where the interests of humans and birds

341   overlap. Additionally the use of a relatively small marine area could be of interest with a

342   view to setting up a marine protected area, protecting the population from future potential

343   fishing conflicts and commercial shipping operating nearby.

344

360

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498 **Tables**

499 Table 1. *Uria aalge* Characteristics of foraging trips recorded by GPS loggers for common

500 murres breeding at Stora Karlsö, Sweden in 2009.

	Mean	SD	
Trip duration (h)	4.20	3.50	a
Distance from breeding-ledge (km)			
greatest	11.77	7.36	b
mean (whole trip)	7.78	5.34	b
Total horizontal distance travelled (km)	26.19	15.81	b
Splash down			
present (proportion of trips) (%)	73		c
duration (h)	0.39	0.48	d
distance from nest at start (m)	320.6	146.3	d
Diving			
number of bouts	5.27	3.84	a
number of dives (whole trip)	34.77	24.26	a
distance of bout from breeding-ledge (km)	9.71	6.29	b
total duration of bouts (h)	1.19	0.74	a
total dive duration (h)	0.83	0.47	a
total inter-dive interval duration (h)	0.35	0.27	a
Surface time (excluding inter-dive pause)			
duration excluding splash-down (h)	2.53	2.84	a
duration including splash-down (h)	2.54	2.92	a
Flight			
number	3.00	1.15	b
duration (h)	0.39	0.26	b
Trip time-activity budget (%)			
bouts, including diving and inter-dive interval	37.33	26.82	b
diving	27.28	19.47	b
inter-dive interval	10.05	7.72	b
splash-down period (when present)	12.56	15.19	e
surface time (including splash-down, but not inter-dive pause)	42.33	36.49	b
surface time (excluding splash-down and inter-dive pause)	35.80	40.67	2
flight	16.21	10.33	b

501 a: 4 individuals, 22 trips; b: 3 individuals, 18 trips; c: 6 individuals, 26 trips; d: 6 individuals,

502 19 trips; e: 4 individuals, 16 trips.

503

504   Table 2. *Uria aalge.* Summary statistics for all flights (105 from 36 trips by 6 birds) during

505   foraging trips of common murre at Stora Karlsö, Sweden (see fig. 6 for comparison of

506   outward and inward flights).

	Mean	SD
Straight line distance (km)	6.31	7.39
Total distance travelled (km)	6.47	7.56
Straightness (total/straight)	1.07	0.24
Speed (ms^{-1})	16.87	4.28
Duration (s)	440.8	446.4
GPS fix number	5.57	5.78

507

508   Table 3. *Uria aalge*. Summary of dives and dive bout characteristics for chick-rearing

509   common murres at Stora Karlsö, Sweden in 2009. Post-dive interval (PDI) based calculations
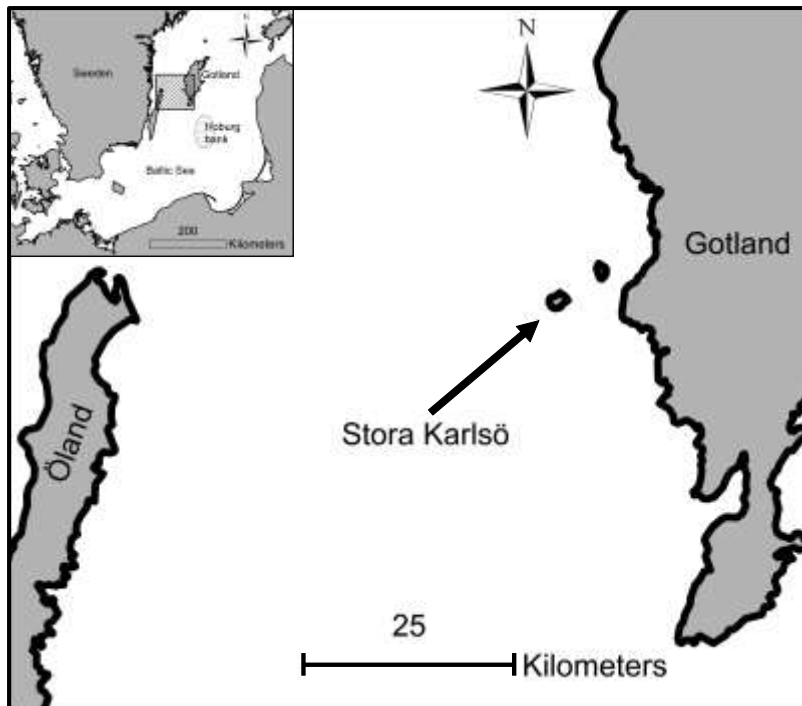
510   use PDIs < 200 s only.

	Mean	SD	
Bouts			
Dive depth maximum (m)	28.46	14.38	a
Duration (s)	803.38	712.08	b
Number of dives	6.99	5.74	b
Dives			
Duration (s)	77.64	28.62	c
Mean of individual maximum recorded depths (m)	62.57	17.67	a
Bottom time duration (s)	41.56	18.86	a
Bottom time/ dive duration	0.52	0.11	a
Vertical descent rate (ms^{-1})	1.10	0.25	a
Vertical ascent rate (ms^{-1})	1.13	0.35	a
PDI (s)	42.9	30.0	c
PDI : Dive duration ratio	2.30	1.11	c
PDI / (dive time + PDI)	0.34	0.12	c
Dive efficiency [bottom time / (dive time + PDI)]	0.35	0.11	a

511   a: 2866 dives from 6 individuals; b: 408 dive bouts from 6 individuals; c: 3326 dives from 7
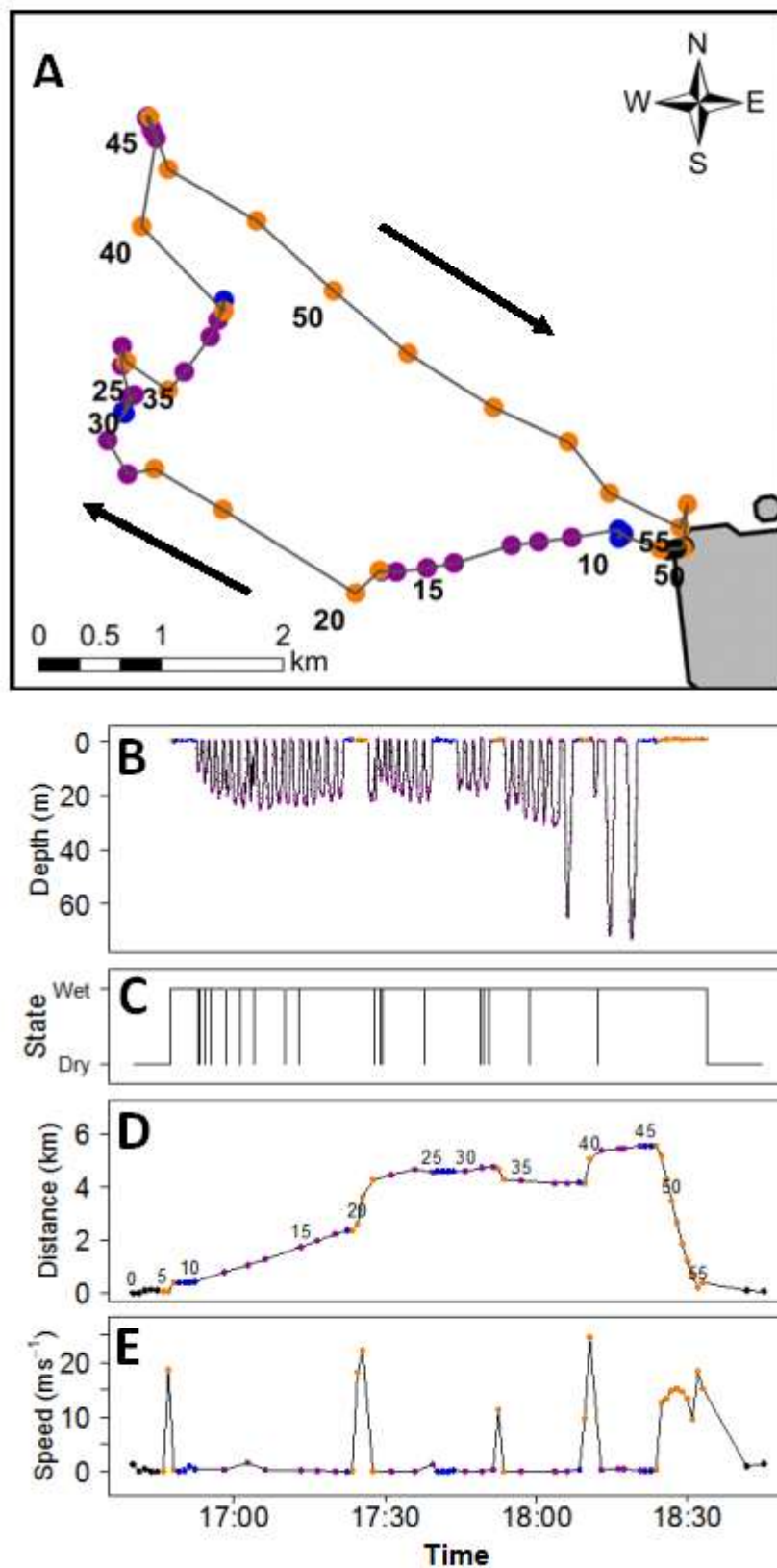
512   individuals.

513

514 **Figures**

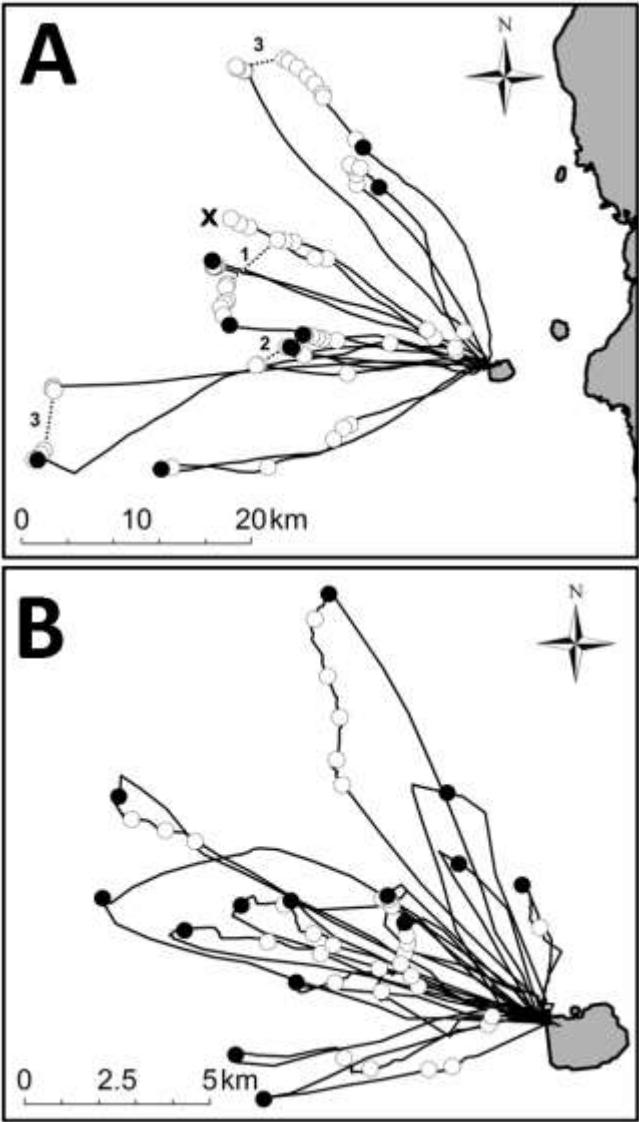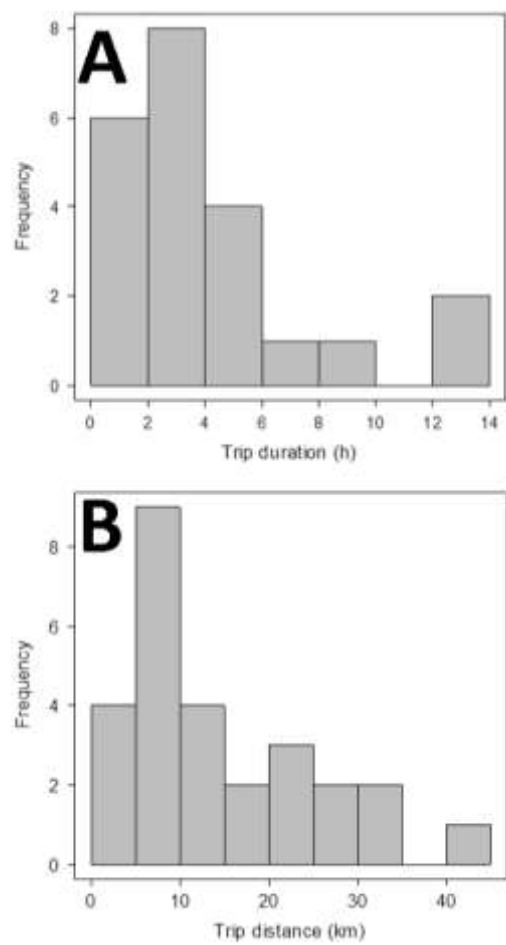515 Fig. 1.

516

517

518   Fig. 2.

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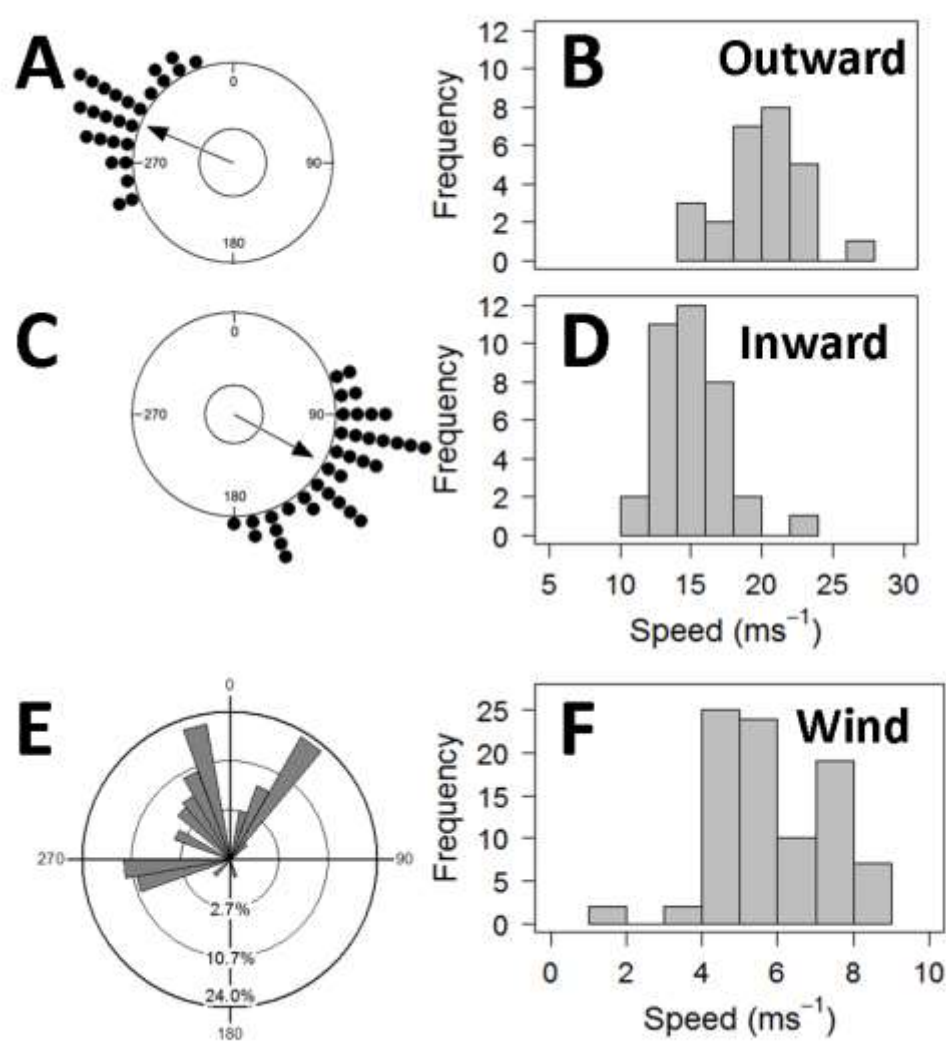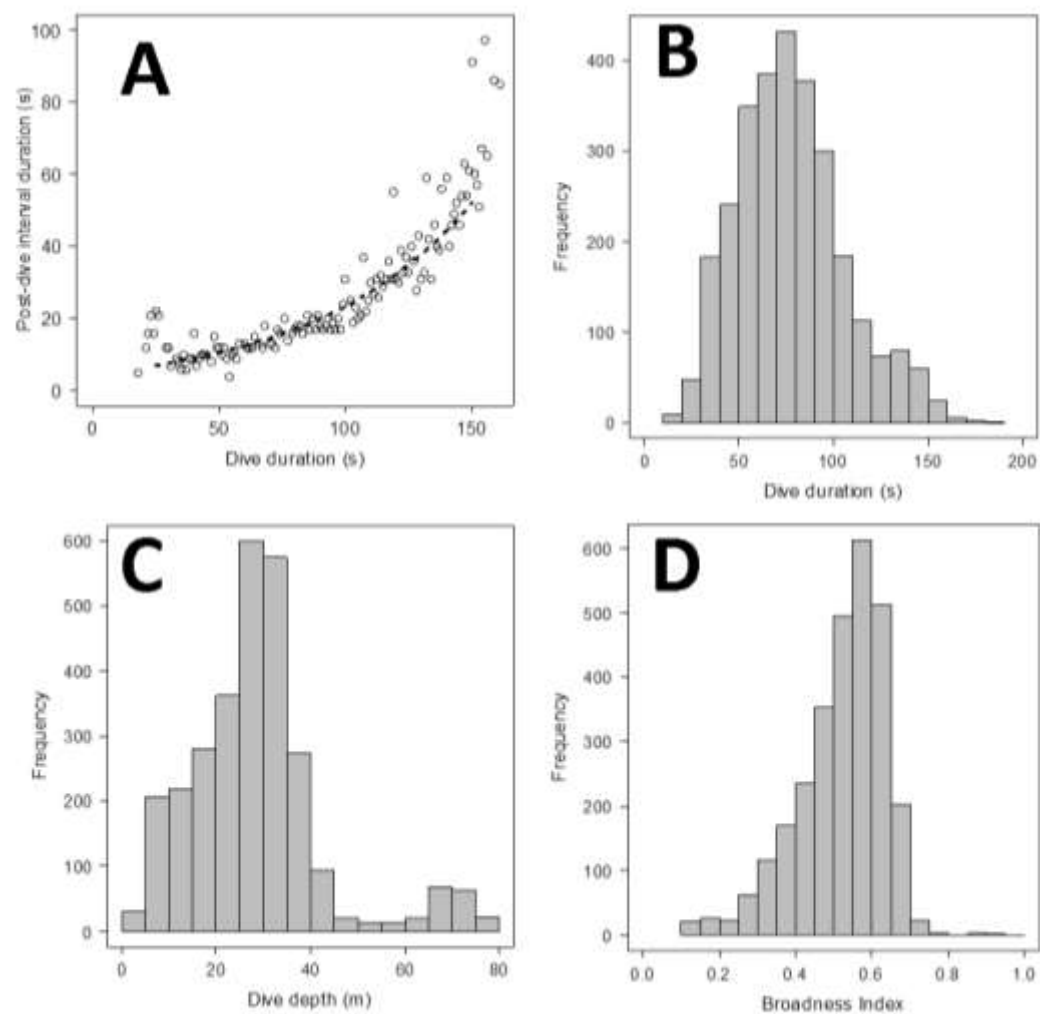
535   Fig. 8.

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537

538 **Figure legends**

539
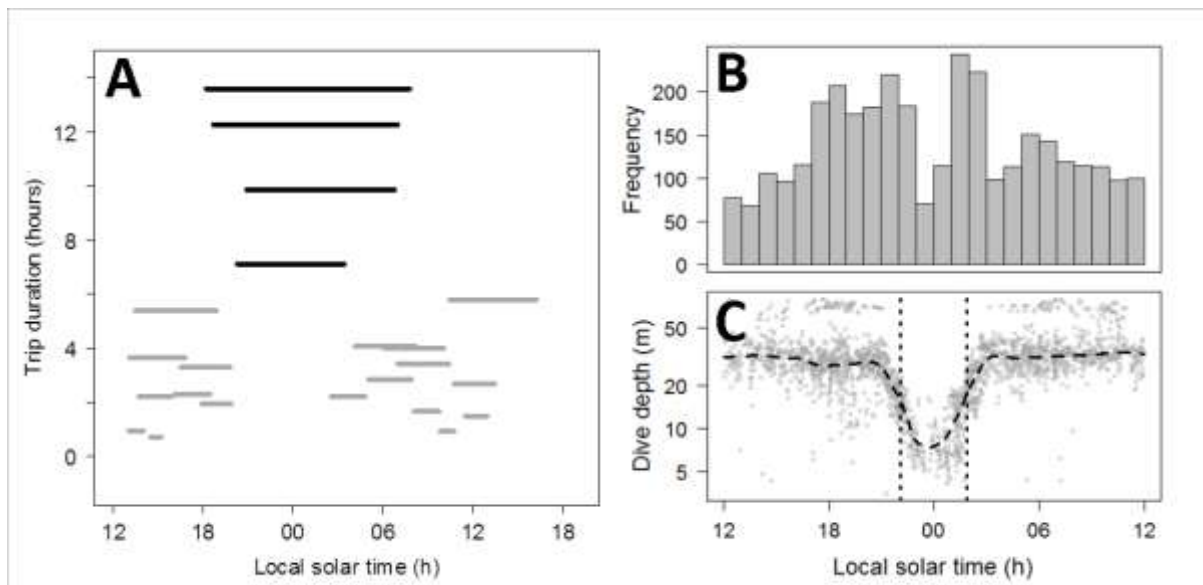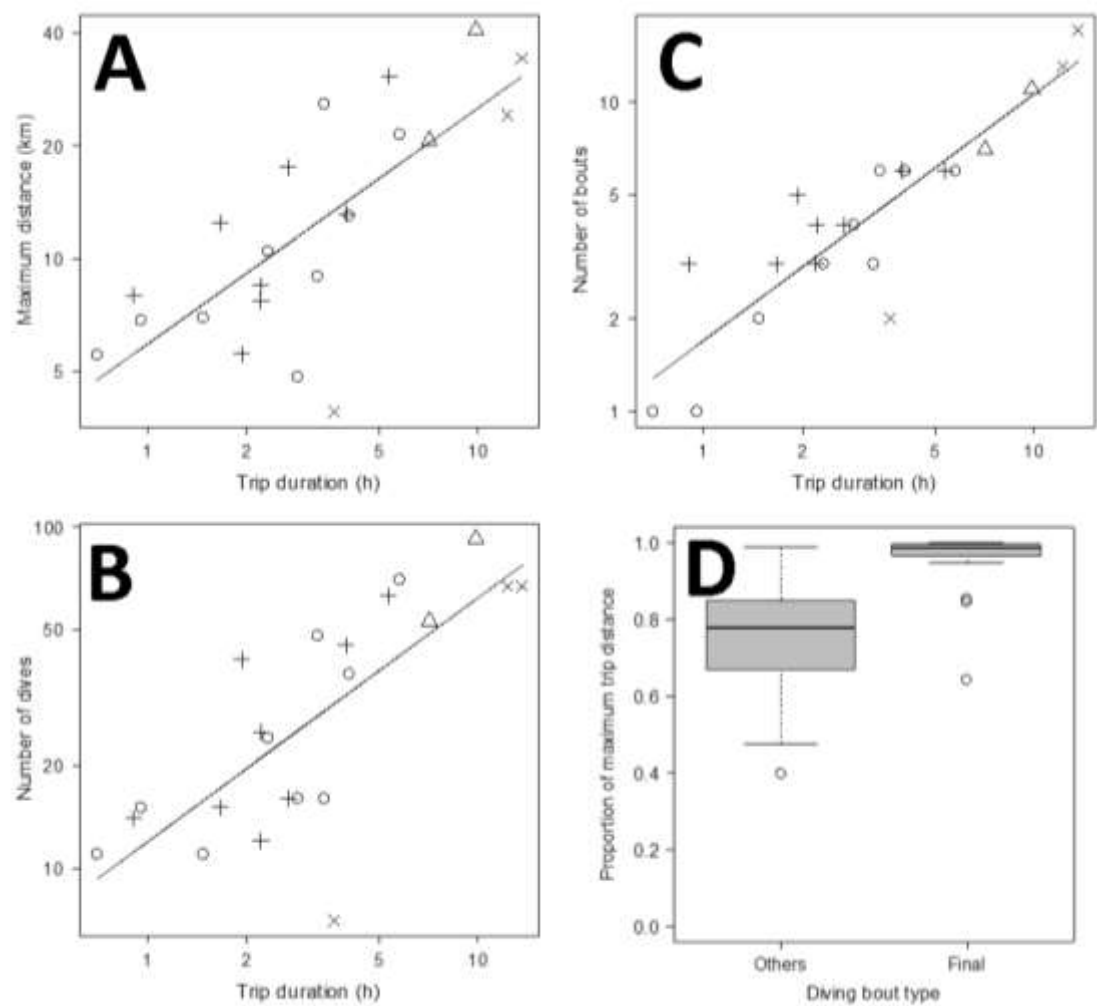
540 Fig. 1. Location of the study colony at the island of Stora Karlsö to the west of Gotland. Land

541 is shaded. The main map is an expansion of the hatched area in the inset map.

542

543 Fig. 2. *Uria aalge. Example of a common murre foraging trip, GPS locations shown (A) and*

544 *arrows to indicate travel direction, then various TDR and GPS parameters (B-E). The*

545 *behaviour classification is indicated by colour throughout; flight (orange), diving bout*

546 *(purple), water surface activity (blue), colony (black). GPS positions are numbered (A & C). B*

547 *shows the depth reading from the TDR device, with dives visible as downward spikes. The*

548 *wet-dry sensor has a lag phase, shortly before 18:30 the bird begins flying (E), but the sensor*

549 *continues to show a 'wet' reading (C); only likely with a wet-dry transition. The distance from*

550 *the island is indicated, D. Instantaneous GPS recorded speed (E), between c. 16:50 and 17:20*

551 *movement occurs (displacement from breeding-colony increases, D), this movement occurs*

552 *during a diving bout, so is not reflected from the surface GPS records (E).*

553

554 Fig. 3. *Uria aalge.* All foraging trips of common murres tracked via GPS, split into long (A,

555 maximum distance from breeding-ledge > 15 km) and short trips (B, maximum distance

556 from breeding-ledge < 15 km). Dive bouts are indicated (open circles) and the final bout of a

557 trip (closed circles). The coastline is indicated by the thick black lines, with land shaded. For

558 four overnight trips (all long trips), there was a period (between 2300 and 0300 CEST) when

559 the GPS devices were not recording, a dashed line is displayed for this period with a number

560 indicating the number of diving bouts occurring during that time. One trip is truncated, due

561 the depletion of the GPS battery (x in A).

562

563 Fig. 4. *Uria aalge.* Frequency histograms of common murre foraging trip duration (A, n = 22)

564 and maximum distance (B, n = 27) from breeding ledge.

565

566 Fig. 5. *Uria aalge.* Foraging activity in common murres by time of day. Trip durations in

567 common murres by trip start time (A) (n = 22), with overnight trips (black) and diurnal trips

568 (grey) indicated. Frequency of dives in one hour bins (B) and depth (log axis) of dives (C, all

569 individual dives shown by small grey open circles) with a smooth line fitted (LOWESS

570 function in R, using 1 hour span). Local solar time (GMT + 1:10) displayed, with sunset and

571 sunrise indicated by vertical dashed lines (C).

572

573 Fig. 6. *Uria aalge.* Foraging trips of common murres, scatter plots of relationship between

574 foraging trip duration and activity (n = 22); maximum distance from breeding-ledge (A,

575 linear regression, t_{22} = 4.94, p < 0.0001), number of dives (B, linear regression t_{22} = 2.74, p <

576 0.0001), and number of dive bouts (C, linear regression t_{22} = 5.60, p < 0.0001). Individuals

577 are indicated by different symbols (open circle, cross, triangle, and x), linear regression lines

578 (broken line) for log-transformed data, displayed with log axis. Box-and-whisker plot (D)

579 comparing distance of final diving bouts to non-final dive bouts, using within trip ratio of

580 dive bout distance to maximum distance from nest reached during trip, ends of whiskers

581 represent the least and greatest values within 1.5 times the lowest or highest quartile

582 (shown by box), values beyond whiskers are shown (open circles), medians at centre line.

583 Final dives occur at significantly greater distances than earlier non final dives (paired t-test, t

584 = 4.47, n = 20, p < 0.001).

585

586   Fig. 7. *Uria aalge.* Summary of resultant vector directions for common murre flights (A & C).

587   The flights are split into outward (A & B) and inward (C & D) movements from the colony

588   (see methods for definitions), with mean flight vector directions in 10° segments for each

589   flight, mean vector shown (A; θ = 298.1°, r = 0.92, z = 22.13, p < 0.001, N = 26. C; θ = 124.2°,

590   r = 0.88, z = 27.82, p < 0.001, N = 36). Flight speeds for outward flight (B, mean 20.0 ± 2.8 m

591   s^{-1}) were greater than inward flight (D, mean 15.1 ± 2.5 m s^{-1}, paired t-test, t = 3.14, df = 20,

592   p = 0.005). Circular plot (E) showing wind heading direction in 10° bins, and wind speed (F,

593   mean 6.3 ± 1.6 m s^{-1}).

594

595   Fig. 8. *Uria aalge*. Relationship between post-dive interval duration (PDI) and dive duration

596   in foraging common murres, with minimum PDI for dive durations at 1 s intervals (A), <150

597   s the relationship can be described by the regression line: Log_e(PDI) = 0.015 (dive duration) +

598   1.68. Dive duration showed a near normal distribution with a slight right skew towards

599   longer dives (B). Histogram of dive depths (C). The proportion of time spent at depth is

600   indicated by the broadness index (D).

601

602

603   **Supplementary material**

604   **S1**

605   **Detailed methods**

606   **Bird-borne data loggers**

607   We used two different devices together: (1) a back-mounted GPSD, and (2) a leg-mounted

608   TDR to record the foraging movements and diving behaviour.

609   (1) The GPSD was an unmodified commercial unit (model GT-120 by Mobile Action

610   Technology, Inc. Taipei, Taiwan) which included a SiRF Star III Low Power chipset and 230

611   mAh battery. This was prepared for deployment by replacement of an outer housing with a

612   heat-sealed plastic sleeve (HSP1-25.4/12.7-X, Hilltop Products Ltd, Warrington, UK; method

613   after Guilford et al.2008), resulting in a cross-sectional area of 3 cm^2 (*cf.* Elliott et al. 2007).

614   The precision of the GPSD was tested by placing on a windowsill in a building imitating poor

615   signal conditions and ran for two days at 50 s intervals. 95 % of positions lay within 65 m

616   latitude and 46 m longitude; 50 % of positions lay within 12 m latitude and 10 m longitude.

617   Instantaneous ground speed recorded by GPSDs is very accurate, often within 0.1 m s^{-1} and

618   a very high proportion within 1 m s^{-1} (*e.g.* Witte & Wilson 2004).

619   (2) TDRs were configured on a conditional logging mode to log pressure only when a salt

620   water switch was on indicating submergence. Log intervals were set to 4 s for all but one

621   device which was 5 s, providing sufficient resolution of dives usually of 30 to 120 s duration

622   (*e.g.* Thaxter et al. 2009).

623   We attached TDRs to an aluminium ring (I.Ö. Mekaniska, Bankeryd, Sweden) mounted on

624   the bird's left leg. GPSDs were attached dorsally along the midline over the bird's centre of

625   gravity, minimising potential effects on balance (Ropert-Coudert et al. 2007). Black Tesa

626   marine tape (product 4651 from Tesa SE, Hamburg, Germany) sealed with a small dab of

627   cyanoacrylate glue, were used to attach devices to body feathers. After device attachment,

628   *c.* 15 mins duration, birds were released near the ledge. When the common murres were

629   released after the deployment, most flew out to sea a few hundred metres, landing on the

630   water surface (TDR and observational data), and returned to the breeding-ledge (<15 mins).

631   We recaptured the common murres after 2 - 10 days.

632   On average 4.5 ± 3.7 trips were tracked per an individual. This resulted in 3281 GPS

633   positions from foraging trips. From these GPS tracked foraging trips we recorded 105 flights

634   with a mean number of GPS fixes per flight of 5.6 ± 5.8. This comprised of 26 outward, 20

635   foraging, and 36 inward flights. The remainder of flights were not classified and were

636   shorter non-foraging trips.

637   TDRs recorded for the complete deployment periods and averaged 4.6 ± 2.4 d (range 2.9 to

638   9.5 d) giving a total period of 765.5 h. 3326 dives were recorded from 7 individuals, 2866

639   excluding the tag with 50 m depth limit. In total 408 dive bouts were recorded, of which 120

640   had GPS positions, 23 being the final dive bouts of foraging trips.

641   **Data treatment and statistics**

642   Flight was classified as where GPS speeds >5 ms^{-1}, chosen as speed followed a bimodal

643   distribution (Fig. S1). Flight durations were calculated as the length of time from the first to

644   the final GPS fix where speeds exceeded 5 ms^{-1}. Then, to adjust for sampling interval, half

645   the interval to the next fix and previous fix was added. Dive bouts were identified as

646   described above. Surface resting was classified as any time that was not any of the other

647   three behaviours. Time activity budgets were calculated as the mean proportion of time

648   spent on each type of behaviour for each trip. GPS signals were impaired at the breeding

649   ledge, due to the high cliff. Hence, recognition of trip start times used a combination of

650   GPSD speed (identifying flight) and wet-dry data (for splashdowns).

651   Data from the GPSDs were mapped in ArcMap (9.3 and 10.0, Environmental Systems

652   Research Institute, Redlands, CA), with which all map figures were produced. Data were

653   initially analysed using the Hawth's Analysis Tools add-in (URL:

654   http://www.spatialecology.com/htools), calculating the distance and bearing between GPS

655   fixes, and the distance from the breeding-ledge. Dive bout positions were calculated from

656   the mean of GPS locations during the bout period. Where no GPS locations were available,

657   the closest (in time) GPS location was used, provided that it was <300 s before or after the

658   bout, and that no large movement had occurred (>250 m between pre- and post-bout

659   position) or birds were in flight.

660

661   Flight segments were separated from the GPS data, where a flight segment included

662   consecutive fixes with speed over 5 ms^{-1} plus the position fix before and after this. For

663   calculations based on speed, only the flight fixes were used; for those involving distance and

664   bearing, the full flight segment was used. The mean speed is the mean of GPS recorded

665   instantaneous ground speeds. Rhumb-line bearing and great circledistance were calculated

666   between first and final position using functions 'bearingRhumb' and 'distHaversine' (Earth's

667   radius 6378137 m) from R package 'geosphere' (Hijmans et al. 2011).

668   We classified flights into three groups. (1) Outward flight, (2) foraging flights, and (3) inward

669   flights. For outward and inward flights we calculate mean speeds and directions which were

670   tested for uniformity with the Rayleigh test (Batschelet 1981). Outward and inward flight

671   speeds were compared for each trip using a paired t-test. The summary for wind conditions

672   provided here (Fig. 6 E & F and text) is for the mean of the conditions experienced for all

673   GPS fixes obtained during flight.

674

675   **References**

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692   over ground. J Biomech 37:1891-1898.

693

694

695   **S2**

696   **Device effects**

697   To assess device effects on study birds, we (1) compared the breeding success of tracked

698   birds with neighbouring untracked pairs and (2) compared the bird weights before and

699   following device deployment.

700

701   **Method.** (1) Throughout the study period, daily observations were made of all pairs

702   breeding on the study ledge to determine the presence of a chick and continuation of

703   breeding. From this the minimum chick age at fledging was calculated (observations began

704   after hatching). Study pairs and control pairs (those not tracked) were compared statistically

705   using Welch's two sample t-test with data checked for normality by Shapiro-Wilk test. (2) At

706   capture (n = 9) and recapture (not all birds were weighed, n = 4) we weighed the murres to

707   ± 5 g using a 1 kg Pesola® spring balance

708

709   **Results.** (1) The mean minimum chick age at first absence was not significantly different

710   between study (mean = 12.9 ± 3.0 d , n = 9) and control (mean = 12.2 ± 3.0 d , n = 37) pairs

711   (Welch's Two Sample t-test, t = 0.55, p = 0.59, df = 11.7) suggesting that fledging success

712   was unaffected.

713   (2) The mean body mass at deployment for all individuals was 921 ± 62 g (n = 9). For four

714   birds for which re-capture weight was also recorded the start weight was 889 ± 73 g and the

715   end weight 869 ± 28 g. The rate of weight change was -12 g d^{-1}, although one bird gained

716   weight (16 g d^{-1}), the other three lost weight (-21 ± 11 g d^{-1}).

717   **Interpretation**

718   Breeding success did not differ between study and control birds. However weight losses

719   were recorded although these were similar to those reported in other studies using

720   biologgers (*e.g.* Benvenuti et al. 2001, Paredes et al. 2008), and this may reflect normal

721   adaptive weight loss (Elliott et al. 2008, Jacobs et al. 2011). Similar device weights were not

722   found to affect dive behaviour (Camphuysen 2005) in a comparison of murres carrying

723   either a 5 g or 23 g, though flight behaviour could be affected (Vandenabeele et al. 2011).

724

725   **References**

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745

746 **Figure S1**

747

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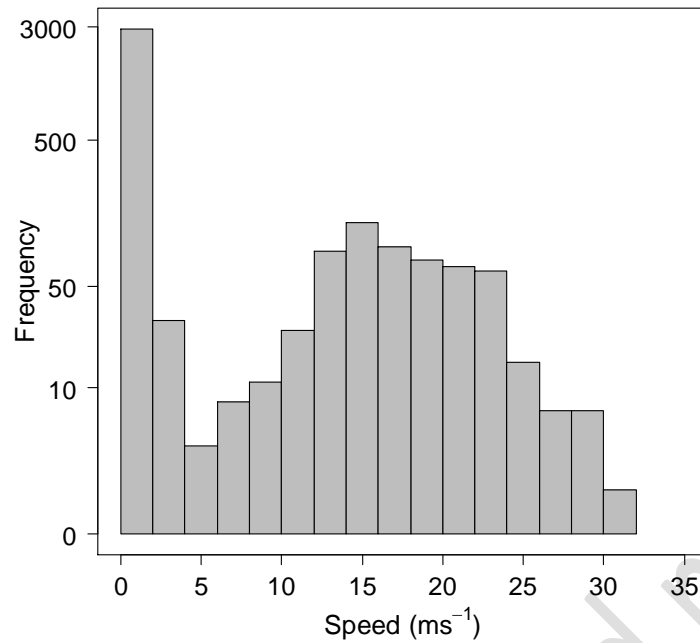
749 *Uria aalge.* Log-frequency histogram of recorded speed for all GPS fixes within foraging trips

750 of common murres, showing a bimodal distribution, >5 m s^{-1} likely to be flight.

751

752