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Published in:
Marine Ecology - Progress Series

DOI:
[10.3354/meps10125](https://doi.org/10.3354/meps10125)

2013

[Link to publication](#)

Citation for published version (APA):
Evans, T., Kadin, M., Olsson, O., & Åkesson, S. (2013). Foraging behaviour of common murrens in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Marine Ecology - Progress Series*, 475, 277-289. <https://doi.org/10.3354/meps10125>

Total number of authors:
4

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

3

4 **Running head**

5 Foraging behaviour of common murre

6

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12

13

14 **Abstract**

15 GPS and time-depth recorders were deployed in combination to investigate foraging
16 behaviour of common murre (*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 murre 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 murre
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⁻¹)

25 ¹) are aided by tailwinds and lower inward flight groundspeeds ($15.1 \pm 2.5 \text{ ms}^{-1}$) 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 murre 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

Final accepted manuscript

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 murrens 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 murren 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 murren during the breeding season. However, if fish numbers are sufficiently depleted
69 by the beginning of the breeding season, murren 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 murren to use a large area of sea to
74 forage. Anecdotal evidence (*e.g.* observations by fishermen) suggests that foraging murren
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 murren 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 murrelets 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 $\log(\text{frequency})$ 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 ¹ (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

245 **Discussion**

246 We found that most foraging parameters measured for common murre in the Baltic Sea
247 were similar to those recorded at other sites, but some findings indicated good foraging
248 conditions for breeding murre. Furthermore, the murre 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.

256 **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 murre (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).

265 **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 murrets 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 murrelets 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 murrelets (Tremblay et al. 2003, also
296 Fig. 4B in Thaxter et al. 2010) that was also found in thick-billed murrelets (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 murrelets
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 murrelets (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 murrelets 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 murre 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 murre 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 murre 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

345 **Acknowledgments**

346 The project was financed by project grants from the Swedish Research Council to S.Å. (621-
347 2007-5930; 621-2010-5584) and a Linnaeus grant (349-2007-8690) from the Swedish
348 Research Council and Lund University to the Centre for Animal Movement Research at Lund.
349 M.K. supported by grants from Formas and Stiftelsen Marcus och Amalia Wallenbergs
350 minnesfond (project MAW 2008.0037). Field work was supported by WWF Sweden. Thanks
351 to Karlsö Jagt- och Djurskyddsförenings AB for their cooperation and help with working on
352 Stora Karlsö island; Länsstyrelsen at Gotland for permissions to carry out the research. Work
353 carried out under ethical permit from Malmö – Lunds djurförsöksetiska nämnd, licence 'M
354 113 – 09'. Thanks to H. Österblom, J. Hentati-Sundberg and E. Willerström and others in the
355 Baltic Seabird Project, who assisted during the field work and gave advice. We thank M.
356 Seaman and three anonymous reviewers for helpful suggestions which have improved this
357 paper. Thanks to Swedish Meteorological and Hydrological Institute (Norrköping, Sweden)
358 for wind data: J. Lage for advice on the use of the MT software for dive analysis. During the
359 fieldwork T.E. was a Masters student at the University of York, UK.

360

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497 extensions in ecology with R. Springer, New York.

498 **Tables**

499 Table 1. *Uria aalge* Characteristics of foraging trips recorded by GPS loggers for common
500 murre breeding at Stora Karlsö, Sweden in 2009.

	Mean	SD	
Trip duration (h)	4.20	3.50	^a
Distance from breeding-ledge (km)			
<i>greatest</i>	11.77	7.36	^b
<i>mean (whole trip)</i>	7.78	5.34	^b
Total horizontal distance travelled (km)	26.19	15.81	^b
Splash down			
<i>present (proportion of trips) (%)</i>	73		^c
<i>duration (h)</i>	0.39	0.48	^d
<i>distance from nest at start (m)</i>	320.6	146.3	^d
Diving			
<i>number of bouts</i>	5.27	3.84	^a
<i>number of dives (whole trip)</i>	34.77	24.26	^a
<i>distance of bout from breeding-ledge (km)</i>	9.71	6.29	^b
<i>total duration of bouts (h)</i>	1.19	0.74	^a
<i>total dive duration (h)</i>	0.83	0.47	^a
<i>total inter-dive interval duration (h)</i>	0.35	0.27	^a
Surface time (excluding inter-dive pause)			
<i>duration excluding splash-down (h)</i>	2.53	2.84	^a
<i>duration including splash-down (h)</i>	2.54	2.92	^a
Flight			
<i>number</i>	3.00	1.15	^b
<i>duration (h)</i>	0.39	0.26	^b
Trip time-activity budget (%)			
<i>bouts, including diving and inter-dive interval</i>	37.33	26.82	^b
<i>diving</i>	27.28	19.47	^b
<i>inter-dive interval</i>	10.05	7.72	^b
<i>splash-down period (when present)</i>	12.56	15.19	^e
<i>surface time (including splash-down, but not inter-dive pause)</i>	42.33	36.49	^b
<i>surface time (excluding splash-down and inter-dive pause)</i>	35.80	40.67	²
<i>flight</i>	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
<i>Straight line distance (km)</i>	6.31	7.39
<i>Total distance travelled (km)</i>	6.47	7.56
<i>Straightness (total/straight)</i>	1.07	0.24
<i>Speed (ms⁻¹)</i>	16.87	4.28
<i>Duration (s)</i>	440.8	446.4
<i>GPS fix number</i>	5.57	5.78

507

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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.

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

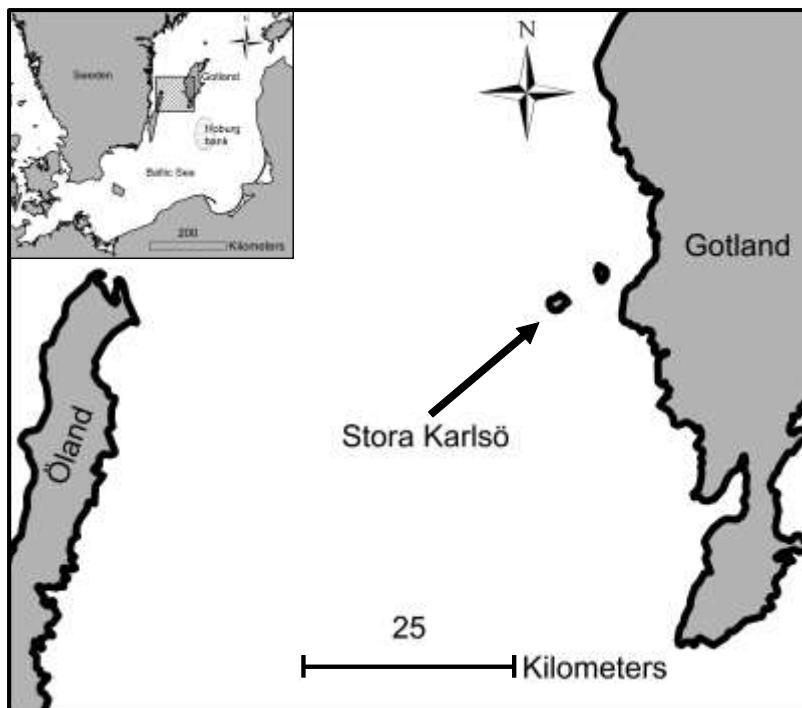
511 a: 2866 dives from 6 individuals; b: 408 dive bouts from 6 individuals; c: 3326 dives from 7

512 individuals.

513

514 **Figures**

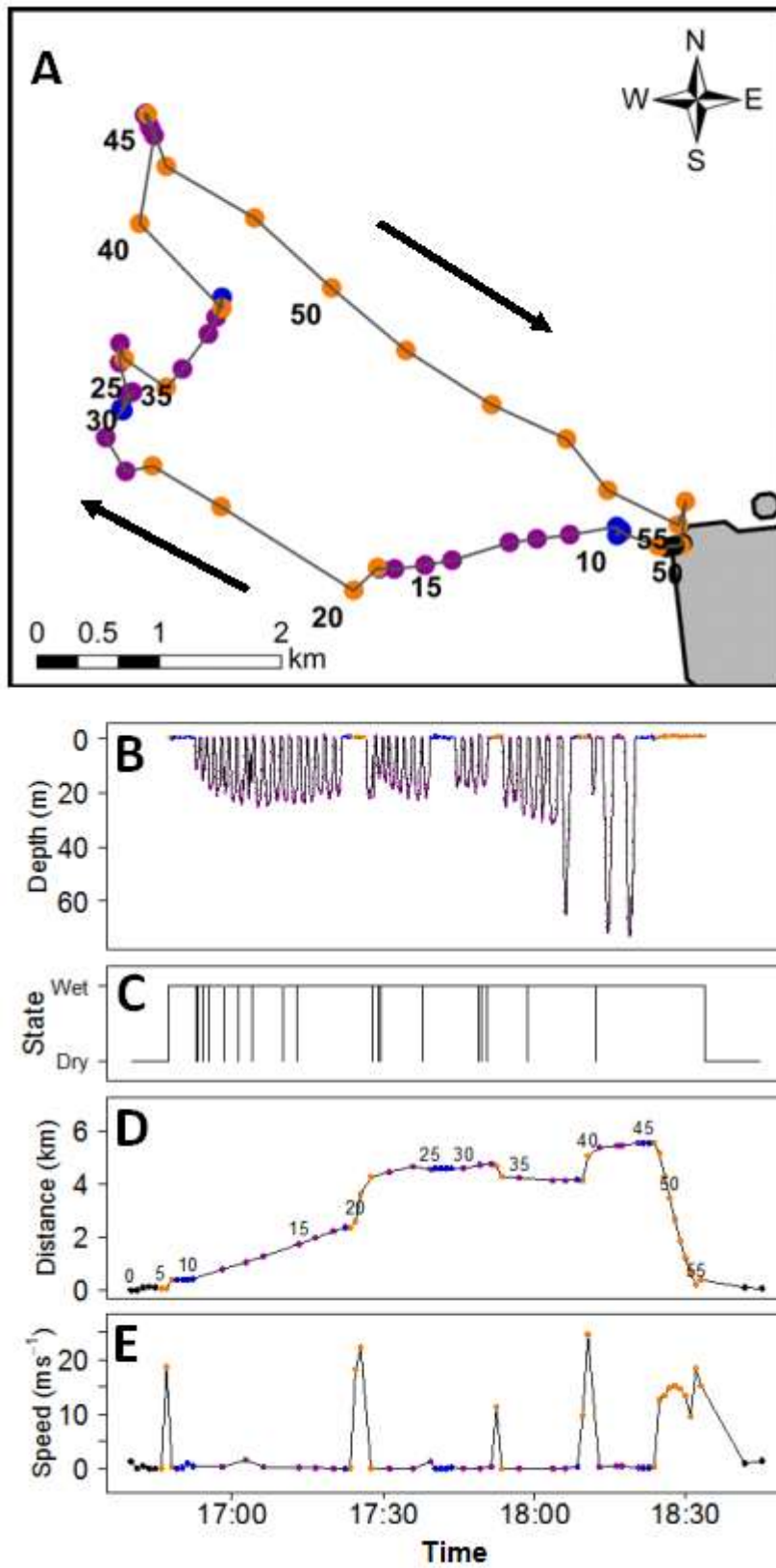
515 Fig. 1.



516

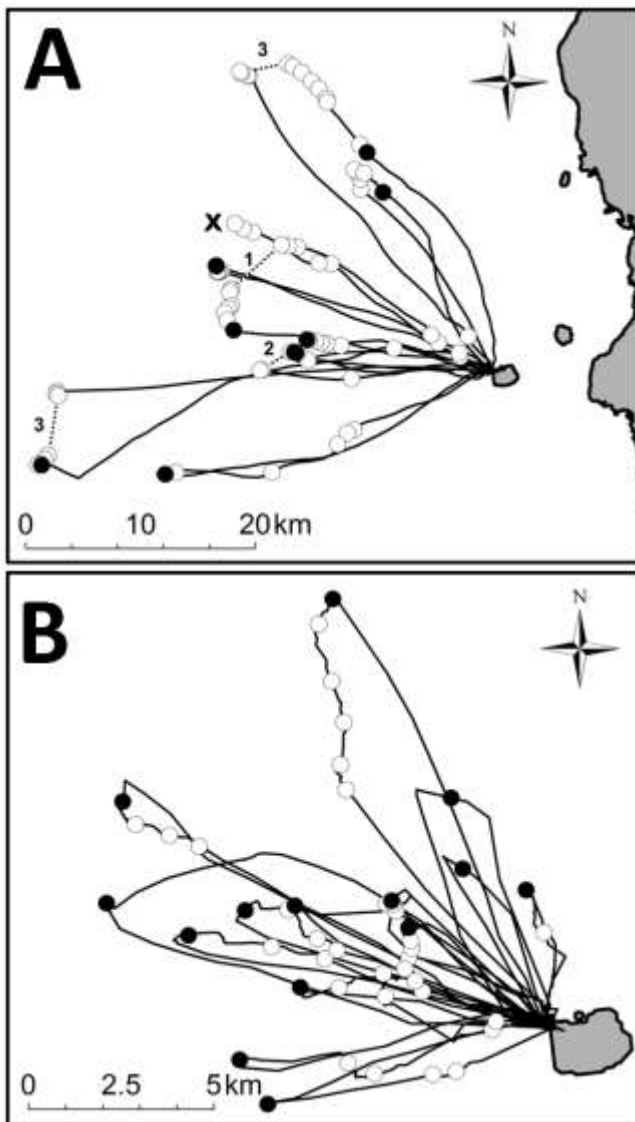
517

518 Fig. 2.



519

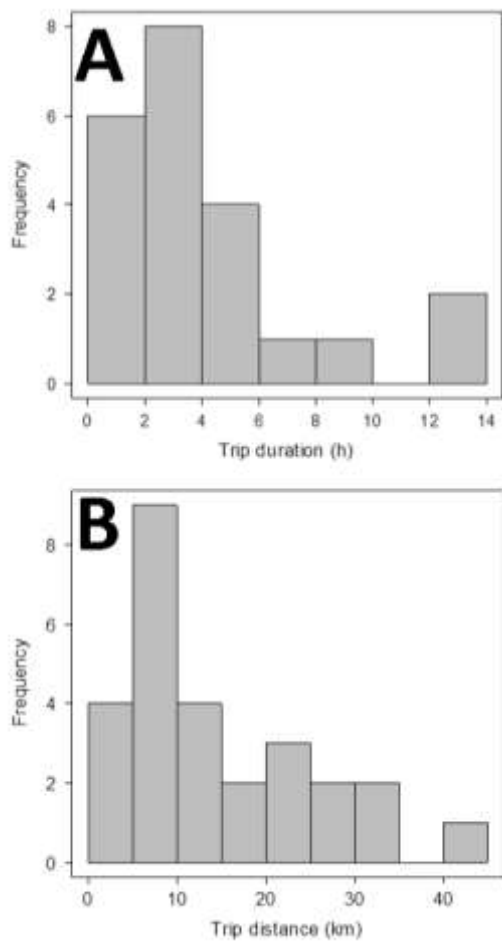
520 Fig. 3.



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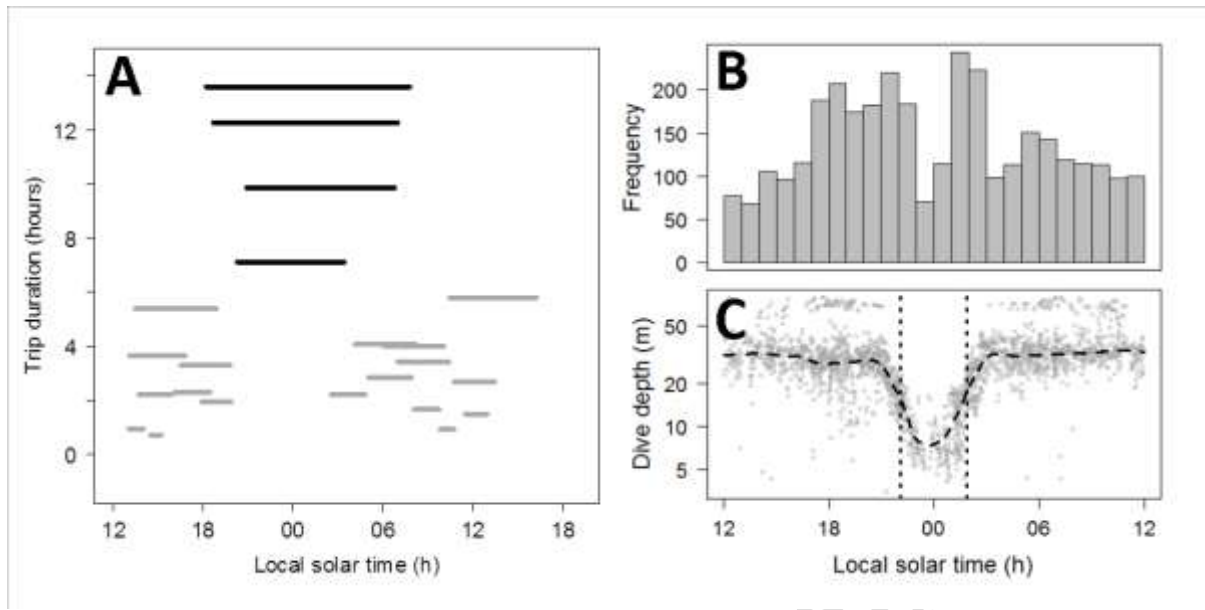
523 Fig. 4.



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526 Fig. 5.

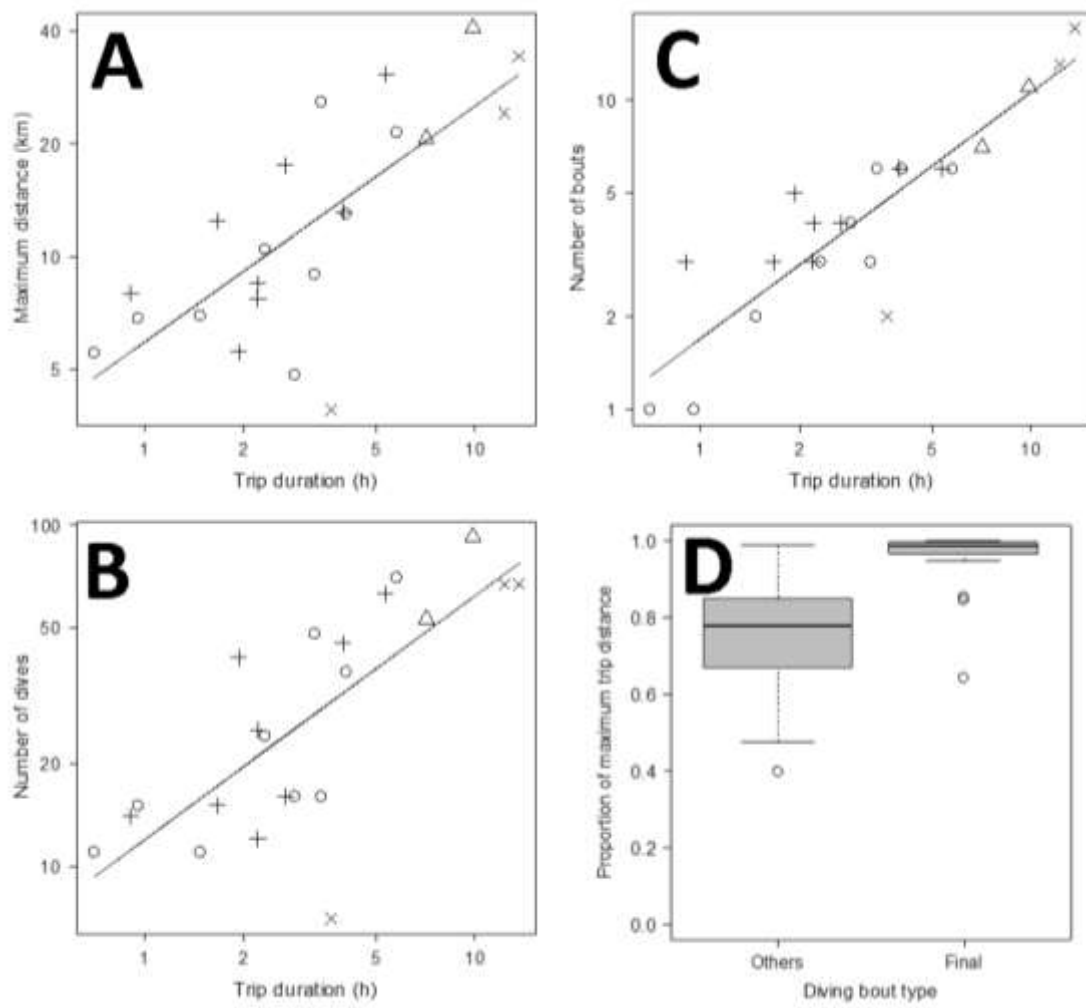


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529 Fig. 6.

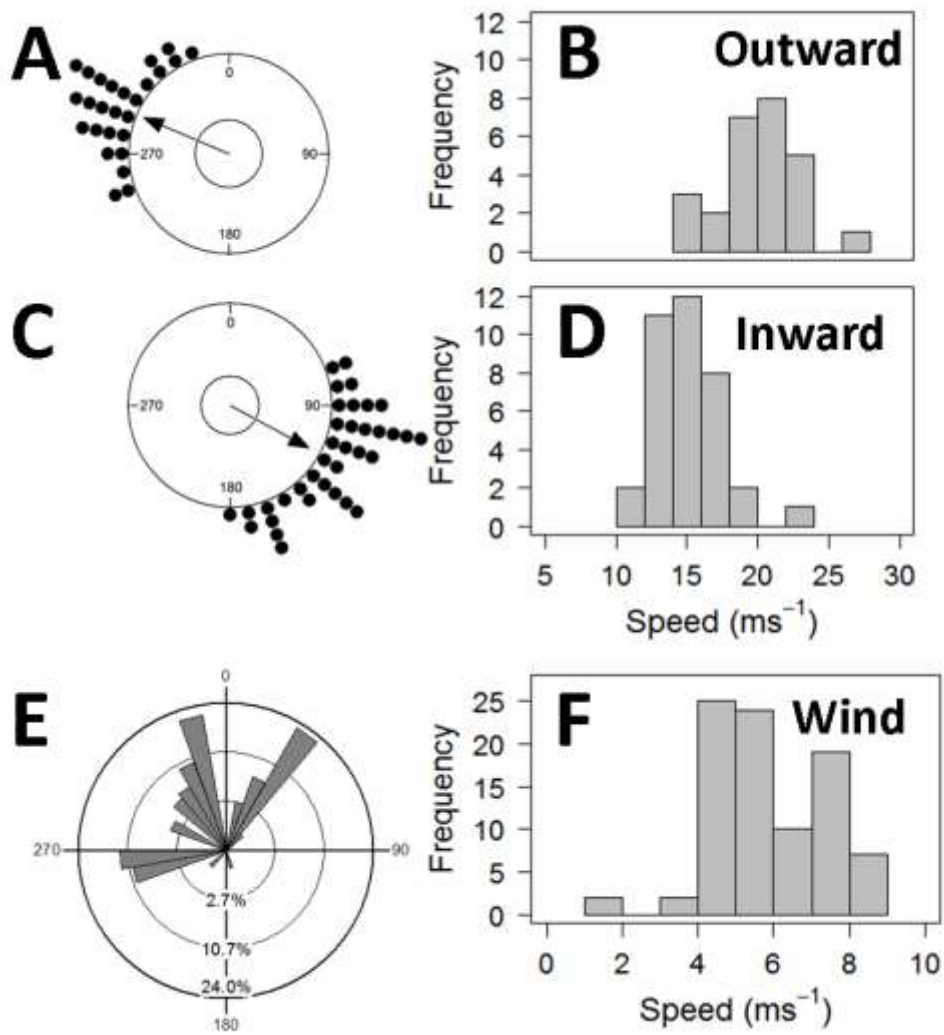


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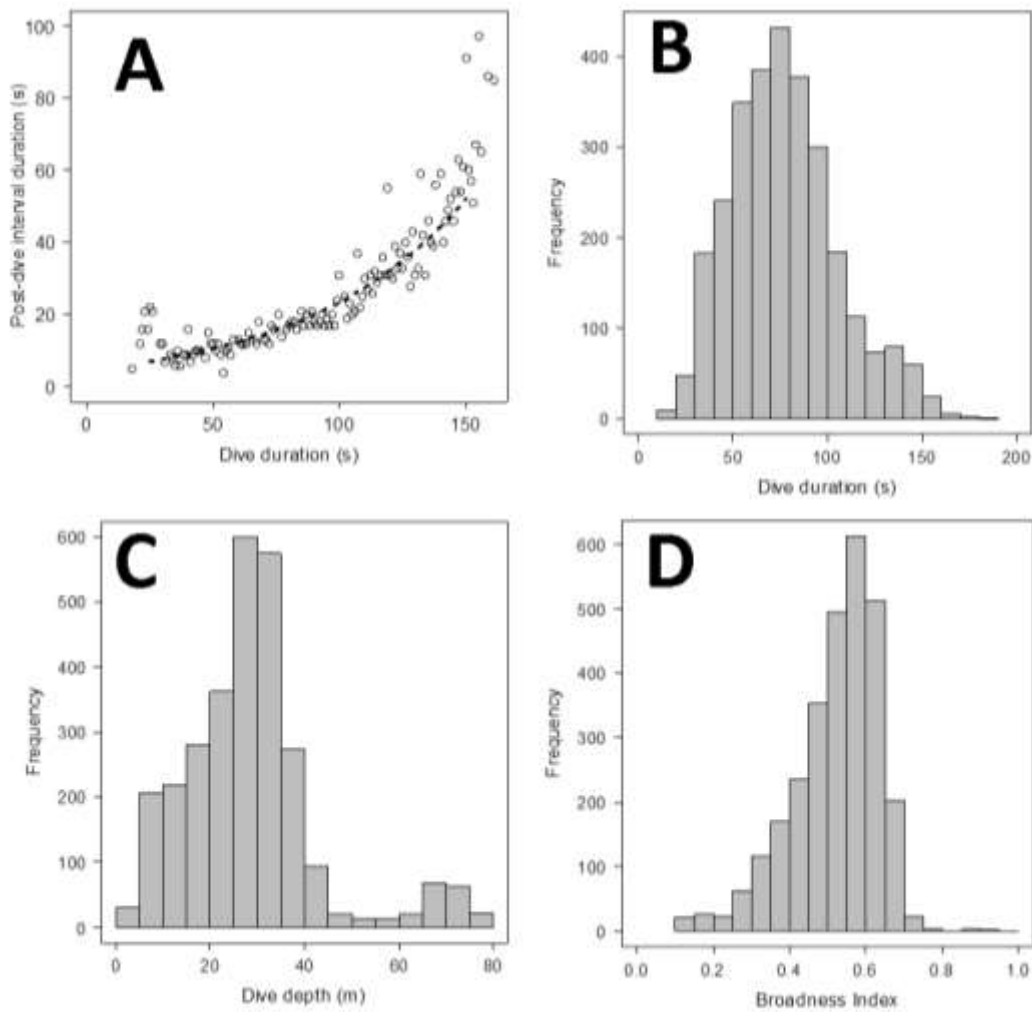
532 Fig. 7.



533

534

535 Fig. 8.



536

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 murre 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; $\theta = 298.1^\circ$, $r = 0.92$, $z = 22.13$, $p < 0.001$, $N = 26$. C; $\theta = 124.2^\circ$,
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: $\text{Log}_e(\text{PDI}) = 0.015 (\text{dive duration}) +$
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 cm² (*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 murrelets 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 murrelets 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 $>5 \text{ ms}^{-1}$, 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.spatial ecology.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

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

724

725 **References**

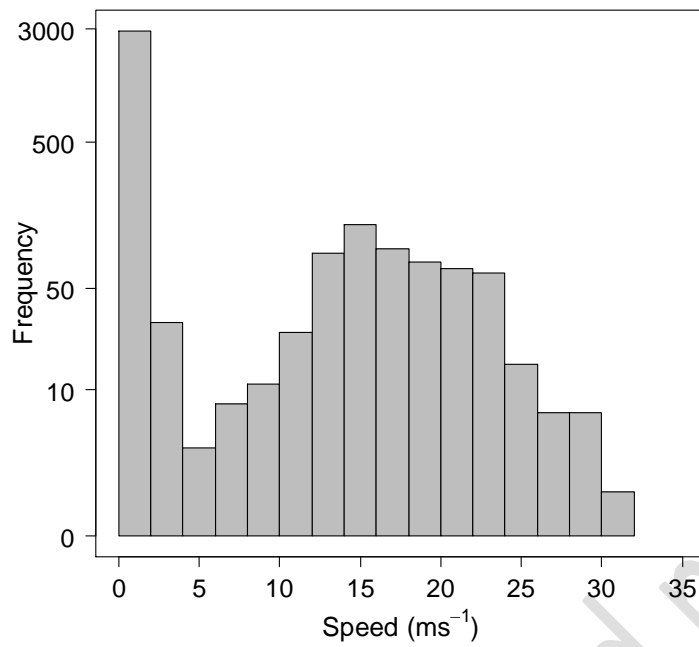
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745

746 **Figure S1**

747



748

749 *Uria aalge*. Log-frequency histogram of recorded speed for all GPS fixes within foraging trips
750 of common murres, showing a bimodal distribution, $>5 \text{ m s}^{-1}$ likely to be flight.

751

752