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

Running head

Foraging behaviour of common murres

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Abstract

GPS and time-depth recorders were deployed in combination to investigate foraging behaviour of common murres (*Uria aalge*) breeding at Stora Karlsö island, Baltic Sea during the chick rearing period. In the pre-breeding period the main prey species sprat (*Sprattus sprattus*) of murres is targeted by commercial fisheries, likely reducing prey availability during the breeding season. Foraging trips typically consisted of a short flight followed by a period sitting on the sea surface (0.39 ± 0.48 h), followed by several (5.3 ± 3.8) diving bouts interspersed by flights and water surface activity. Following the final diving bout murres returned directly to the colony. Overnight foraging trips lasted longer than daytime trips and that corresponded with greater diving activity and reduced dive depths around dawn and dusk, likely times of high prey accessibility. High outward flight groundspeeds (20.0 ± 2.8 ms^{-}

^{1}) are aided by tailwinds and lower inward flight groundspeeds (15.1 ± 2.5 ms^{-1}) impeded by headwinds. Flights following the wind direction may reflect a strategy to reduce crosswind drift. Foraging intensity was lower than reported by most other studies of murres suggesting more abundant or aggregated prey.

Keywords

Foraging behaviour, diving behaviour, *Uria aalge*, common murre, wildlife telemetry, data loggers, Baltic Sea

Introduction

To understand the breeding ecology and behaviour of seabirds it is necessary to study their behaviour both at the breeding colony and at sea. At the colony, detailed visual observations can be made, at sea visual observation can only provide brief snapshots of behaviour and the individual colony of origin and the breeding status of individuals are unknown (*e.g.* Scott 1990, Davoren et al. 2002). In recent years, the development of miniaturised electronic devices has allowed recording of detailed behaviour at sea (reviewed by Burger & Shaffer 2008). Studies on alcids were conducted with regard to both spatial (*e.g.* Benvenuti et al. 1998, Thaxter et al. 2009) and diving behaviour (*e.g.* Tremblay et al. 2003, Paredes et al. 2008). In this paper we describe how two commercially available devices were used simultaneously to record both diving activity and spatial activity in a large alcid, the common murre (*Uria aalge*).

As single prey loaders, chick-rearing adult murres return from foraging trips with one fish held length-ways in the beak to feed to the chick (Bradstreet & Brown 1985), limiting foraging range when chicks are fed several times a day. This may lead to local depletion of fish populations near the colony and puts pressure on birds to travel further to forage at larger colonies, termed 'Storer-Ashmole's halo' (Ashmole 1963 reviewed in Elliott et al. 2009a, Gaston et al. 2007). By combining GPS and time-depth recorder (TDR) devices it is possible to determine the positions of final diving bouts, *i.e.* where the prey is captured for a chick.

In the Baltic Sea, a large-scale shift has occurred from a cod (*Gadus morhua*) dominated to sprat (*Sprattus sprattus*) dominated ecosystem. This may have occurred due to a combination of anthropogenic drivers, such as fishing pressure and eutrophication, and climate change with sprat numbers increasing following reduced predation by cod (MacKenzie et al. 2002, Casini et al. 2009, 2011, Möllmann et al. 2009). Common murres in the Baltic Sea are heavily dependent on sprat (Lyngs & Durinck 1998). Thus, this change in the dominant species meant a strong increase in prey abundance, but also a reduction in prey condition and weight, resulting in a reduction in prey quality (Österblom et al. 2006, Casini et al. 2011). In recent years, when the cod fishery was reduced, cod numbers have started to recover. At the same time fishing pressure on sprat has increased resulting in a decrease in biomass of *c.* 30% since a peak in the late 1990s (ICES 2010). However, on the scale of the Baltic Sea, sprat abundance is still high in comparison with the 1970s and 1980s when numbers were at approximately one third of 2009 levels (ICES 2010). The sprat fishery near Stora Karlsö practically ceases from June to August, so it is not in direct competition with murres during the breeding season. However, if fish numbers are sufficiently depleted by the beginning of the breeding season, murres may have high foraging effort, with rapid depletion of fish close to the island. Alternatively, fish numbers are not reduced to low levels, but as sprat disperse following spawning, requiring more effort to catch, a commercial fishing operation may cease to be economically viable. If this reduced aggregation influences the birds, we would expect murres to use a large area of sea to forage. Anecdotal evidence (*e.g.* observations by fishermen) suggests that foraging murres from the Karlsö islands use a wide area and concentrate off the northern tip of Öland and south of Gotland at the Hoburgs Bank (Fig. 1).

In this paper we describe the foraging behaviour of chick rearing common murres using simultaneous GPS device (GPSD) and TDR deployment. The study aimed to gain a broad picture of foraging activity at Stora Karlsö, recording foraging locations, temporal patterns, and foraging strategies. The detailed data allows a fine-scale analysis of activity during foraging trips, as well as whether multiple foraging sites are used during a trip and the behaviour at the start of a trip. The GPS data allow foraging flights to be analysed, including how these may be affected by wind. We hypothesise that foraging routes and locations are affected by wind speed and direction. We predict that foraging activity will be concentrated around dusk and dawn, as has been found for several other locations (*e.g.* Regular *et al.* 2010). This population has relatively high reproductive output (*e.g.* fledging success 0.88 – 0.97 in years prior to study) and a stable or increasing population size (Kadin et al. 2012, unpublished data) and therefore we expect that foraging and diving effort will be equivalent or lower to other murre colonies. This is the first study describing the foraging strategies of common murres in the Baltic Sea.

Methods

Study site and species

The study took place at Stora Karlsö island, Sweden (57˚17’ N, 17˚58’ E), in the south-eastern Baltic Sea (Fig. 1). Some 8000 pairs (Österblom et al. 2002) of common murres (*Uria aalge*, Pontoppidan 1763) breed here, somewhat more than the neighbouring island of Lilla Karlsö (Lyngs 1993). Field work took place from the 9 - 20 June 2009; with devices deployed from 9 - 15 June 2009. Common murres are present at the breeding colony during late winter, with daily presence from mid-April, when the breeding period begins. Experienced birds typically show both high site and mate fidelity (Moody *et al.* 2004). In mid-April mating occurs, *c.* 15 d later a single egg is laid (Hatchwell & Pellatt 1990). After hatching, both parents provision the chick (Kadin et al. 2012), with *c.* 3 - 5 feeds d^{-1} (Österblom & Olsson

2002, Thaxter et al. 2009). At 15 – 30 d the still flightless chick leaves the colony accompanied by the male parent on whom it continues to depend on for over a month (Scott 1990). Breeding adults were caught from the same natural rock ledge sited directly beneath an artificial breeding cliff structure (described by Hentati-Sundberg et al. 2012). At the base of this structure was a trapdoor in the floor, through which we caught the birds by using a noose pole.

Bird-borne data loggers

We used two different devices together: a back-mounted GPSD (model GT-120 by Mobile Action Technology, Inc. Taipei, Taiwan) and a leg-mounted TDR (model LAT 1500 by Lotek Wireless, Ontario, Canada) to record the foraging movements and diving behaviour (detailed description in S1 in the supplement at ******). Eight GPSD were deployed, half were set to record every 90 s, the others every 60 s, all but two were set to turn off from 2300 h to 0300 h local time (time in CEST unless stated), to save power at a time when activity was expected to be low (*e.g.* Regular et al. 2010). Two versions of the TDR were used, either with 50 (n = 3) or 500 m (n = 8) depth limits. All GPSD deployments included a TDR, but three TDR were deployed without a GPSD, resulting in eight GPSD with TDR deployments, and three TDR only deployments. We attached an identification ring to the right leg of the bird, following the Swedish Bird Ringing Centre scheme (Naturhistoriska riksmuseet, Stockholm). The TDR was then mounted on an aluminium leg ring. With the GPS attached to back feathers using several strips of black Tesa marine tape (product 4651 from Tesa SE, Hamburg, Germany). Total weight of bird-borne instrumentation (including identification ring, attachments and devices) was *c.* 29 g equivalent to *c.* 3 % (range 2.9 – 3.8 %) of body weight for the study birds.

Owing to some deployments with both GPSD and TDR and others with only TDR, it was necessary to use different parts of the data-set depending on the analysis. Thus, sample sizes differ depending on the factor of interest. We recovered devices from 7 common murres tracked during the breeding period. Six of GPSD with TDR, and one TDR only; the remaining four birds were not recaptured, so devices could not be recovered. However, these birds were observed on the breeding-ledge apparently continuing chick provisioning. There were three 60 s and three 90 s interval GPSDs. One 60 s and one 90 s devices failed for unknown reasons after 4 and 12 h, respectively. The remaining 4 devices recorded on average for 53 and 58 h for the 60 s and 90 s devices, respectively. In total 27 foraging trips were tracked, of which 18 were complete, 22 included at least the start and end of the trips; the remaining 5 missed the start or end positions (detailed sample sizes in S1).

Data treatment and statistics

TDR data were analysed in MultiTrace-Dive (Jensen Software Systems, Laboe, Germany) to recognise and parameterize each dive and sequence of dives, *i.e.* a dive bout. An activity was classified as a dive when having a maximum depth of at least 3 m (after Paredes et al. 2008); the start and end of a dive was set when 5 % of the maximum dive depth was exceeded or reached, respectively. The bottom-phase of the dive, which roughly represents the portion of the dive spent actively foraging, was defined as time >75 % maximum dive depth (Tremblay et al. 2003, Halsey et al. 2007). We calculated various measures for each dive, including dive duration, maximum dive depth, and vertical ascent and descent rates. To investigate the minimal recovery period following dives, data were pooled, and minimum post-dive interval (PDI) values taken for each dive duration at one second resolution was plotted against dive duration (Fig. 8 A). Dive efficiency was calculated as (Camphuysen et al. 2005):

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

Dive bouts, “periods of sustained diving activity” (Thaxter et al. 2010), are a sequence of dives with only brief PDI. Definitions of dive bouts differ, generally using either a fixed criterion, or varying, for example using both differences in dive depths and PDI (*e.g.* Mori et al. 2001). Here the method of Sibly et al. (1990) was applied to calculate a fixed maximum PDI providing a bout ending criterion (Paredes et al. 2008, Hedd et al. 2009), plotting log(frequency) against PDI using the R statistical environment (R Development Core Team 2010) with package ‘HyperbolicDist’ (Scott 2009). A natural cut-off indicating the end of a bout was 250 s. Various measures were calculated for dive bouts, e.g. number of dives and mean maximum dive depths.

We analysed foraging trips using a combination of GPSD and TDR data, which allowed trip start and end times to be determined. We classified behaviour during trips into four categories; (1) diving bouts, (2) splashdown, (3) surface resting, and (4) flight (see S1). ‘Splashdown’ periods were recognised as the first uninterrupted (*i.e.* with no flight or diving) period of water surface activity (Burger 1997, Davoren et al. 2003).

Data from the GPSDs were mapped in ArcMap (9.3 and 10.0, Environmental Systems Research Institute, Redlands, CA), with which all map figures were produced.

To compare the distance from the colony of final dive bouts, and the rest of dive bouts (non-final dive bouts) occurring during each foraging trip, we calculated the ratio of the distance from the breeding-ledge for a dive bout to the maximum distance reached during a trip. To compare final bouts with non-final bouts, the mean ratio was calculated for non-final dive bouts for each foraging trip, producing an index, allowing comparison irrespective of actual distances. In a paired t-test these two values were compared with all foraging trips pooled.

To examine how trip duration relates to activity on foraging trips, we looked at, (1) the maximum distance from the colony reached, (2) number of dives, and (3) the number of bouts per a foraging trip. Although time of day is likely to affect activity (*e.g.* Fig. 5), this was not included in our models because of the small sample size. We developed linear mixed-effects models (LMMs) with individual as a random effect. Model selection and validation followed that outlined by Zuur et al. (2009), using the 'nlme' package (Pinheiro et al. 2011) in R.

Flight segments were separated from GPS data (see S1) to analyse flight activity. Amongst other parameters we calculated ground speed, the speed of the bird relative to the ground, as opposed to ‘air speed’, the speed travelled relative to the air mass. We classified flights into three groups. (1) Outward flight included flights between breeding-ledge departure and the first diving bout (this included the flight both before and after a splashdown). (2) Foraging flights were any flights during a trip that occurred after the first dive bout and before the final dive bout. (3) Inward flights took place from the final dive bout to arrival at the breeding-ledge. Wind data from a nearby weather station (70 km from the study site at the north point of the island of Öland, fig. 1) gave the median wind direction in 10° bins and mean wind speed at 1 ms^{-1} resolution, both in 3 hour blocks.

We looked at possible device effects on the study birds, through weight change and breeding success (in the supplement, S2, at ******).

Figures were generated and statistical analyses performed with R (R Development Core Team 2010), except for the maps which were produced in ArcGIS. Some circular statistics and figure 7 parts A, C and E were generated with Oriana (Kovach Computing Services, Pentraeth, Anglesey, UK).

Results

Foraging trips and time activity budget

Foraging trips usually started with a short flight to a splash-down period, before the birds either dived or flew to a foraging site then dived (see Fig. 2 and 3). Dives occurred in short sequences, bouts, with short PDI. Several dive bouts occurred per trip sometimes with short flights between these. After the final dive, birds usually flew directly to the breeding-ledge, presumably to feed their chick although this was not systematically observed. This final dive bout generally occurred close to the maximum distance from the breeding-ledge (Fig. 3 & Fig. 6 D).

During foraging trips a high proportion of time was spent on the sea surface (>40 %), with slightly less time actively foraging in dive bouts (<40 %). The remaining time (<20 %) (Table 1) was dedicated to flight. During dive bouts, approximately a quarter of the time was spent recovering during PDIs. Trip durations were variable (Fig. 4 A), with a median value of 3.1 h, somewhat less than the mean value (Table 1), suggesting many shorter trips with few much longer trips. Trips with evening departures were typically longer in duration than daytime trips (Fig. 5 A). Four out of five trips occurring after 1900 h were >6 h, and no trip >6 h started between midnight and 1900 h. The longer the duration of a foraging trip, the greater the maximum distance reached from the breeding colony (Fig. 6 A). This relationship did not appear to differ among individuals. LMMs included individual as a random effect with random intercept and slope or random intercept only both were less parsimonious (higher AIC values).

Diving activity increased with trip duration, both the number of dives (Fig. 6 B), and the number of dive bouts (Fig. 6 C). For both factors, the most parsimonious model did not include individual (selected by AIC) suggesting that little variation was explained by individual. Trip duration (Fig. 4 A) and the maximum distance from the breeding-ledge reached during trips (Fig. 4 B) showed great variation, though distance was more uniform in distribution. The total distance travelled (Table 1) was only slightly more than double the maximum distance reached (mean ratio 2.26 ± 0.20), indicating that routes followed were direct (Fig. 3), with straight flights too (Table 2).

Flight behaviour

Flights were of intermediate distance, being several km and generally <500 s (Table 2). Flight ground speeds recorded by the GPSD were very variable ranging from *c.* 5 m s^{-1} up to 32 m s^{-1} (Fig. S1 in supplementary material at *****), this reflecting (1) the variation in air-speed, (2) wind conditions (Fig. 7 E & F), (3) or a combination of these. Outward flights mostly occurred over a fairly narrow sector to the north-west of the island (Fig. 7 A). The mean ground speed during outward flights was greater than during inward flights (Fig. 7 B, D), with outward flights typically having a tailwind component and inward flight a headwind.

Diving behaviour

Dive depths followed a bimodal distribution (Fig. 8 C) but dive duration (Fig. 8 B) showed a unimodal distribution. Dive parameters are summarised (Table 3). The majority of dives were U shaped with a broadness index mostly >0.015 (the V-shape threshold; Halsey et al. 2007) (Fig. 8 D). Therefore, dive shapes were not analysed further. The minimum surface recovery period, PDI value, increased with dive duration with a steep increase beyond 150 s (Fig. 8 A). On average the dive time was slightly more than double the PDI (Table 3). Diving frequency was greatest in the evening (Fig. 5 B), from 1700 h - 2300 h (local solar time), and around dawn (0100 h – 0300 h). Mean dive depths were near constant from 0300 h - 2100 h, but then reduced from 2100 h – 0300 h reaching a minimum around midnight (Fig. 5 C).

Discussion

We found that most foraging parameters measured for common murres in the Baltic Sea were similar to those recorded at other sites, but some findings indicated good foraging conditions for breeding murres. Furthermore, the murres used a limited foraging area suggesting that prey was aggregated rather than dispersed. Alternatively the wind conditions may have influenced the use of foraging areas. However, our study period was limited and thus may not be representative of the general conditions throughout the season or between years. These detailed insights into foraging behaviour add to our understanding of murre foraging. For example, the possible use of a bimodal foraging strategy, with long overnight trips, and shorter daytime trips , a behaviour that would be less apparent in studies relying on TDRs alone.

Splashdowns

Most foraging trips began with a splashdown period where birds landed on the water surface close to the colony, a similar pattern to that of other studies of common and thick-billed murres (Burger 1997, Elliott et al. 2009b). This suggests that splashdowns are important, although their primary function is debated. It may offer the opportunity to clean plumage (Elliott et al. 2009b), but may also play a role in determining foraging direction as departing birds observe the direction of incoming birds (Burger 1997). A similar behaviour has been observed in breeding colonies of Guanay cormorants (*Phalacrocorax bougainvillii*) (Weimerskirch et al. 2010).

Foraging distance and duration

The duration and maximum distances of foraging trips observed at Stora Karlsö is comparable to those measured in other studies (*e.g.* Tremblay et al. 2003, Thaxter et al. 2010), though trip duration was short in 2009 (Kadin et al. 2012). Stora Karlsö is a relatively small colony compared to other sites, where tens of thousands of pairs are not uncommon, thus competition may be relatively low. There may also be less intra-specific competition compared to other colonies, with few large colonies nearby, although there may be inter-specific competition with razorbills of which there are similar numbers to murres at Stora Karlsö (Hedgren & Kolehmainen 2006) and with smaller populations on the neighbouring island of Lilla Karlsö (Lyngs 1993).

Flight behaviour and wind

Murre foraging flights largely occurred on the same axis as winds, with outward flight with tailwinds and inward flight into headwinds. This could represent a strategy to reduce crosswind wind drift over the sea where a fixed frame of reference thought necessary to assess drift is unavailable (Åkesson & Hedenström 2007). However partial compensation for wind drift may be possible by: (1) Maintaining optical flow (the time taken for an object to pass across the retina) by selecting flight altitude, as used by some insects over land and water (Riley et al. 1999, Srygley & Dudley 2008). (2) Using the ‘wave landscape’, the pattern of waves over the sea as a fixed reference which could allow for partial compensation as the wave patterns would change slower than wind speeds (Alerstam & Pettersson 1976). (3) Using coastline as a fixed reference (e.g. Åkesson 1993). Preferences for headwinds were observed for alcids at sea (Spear & Ainley 1997), with their high airspeed associated with high wing loading, avoidance of headwinds for energetic reasons may be reduced given orientation advantages (drift avoidance) of avoiding crosswind conditions, though high wind speeds have been shown to increase energy expenditure by auks (Furness & Bryant 1996).

Dive activity

The mean maximum dive depths of common murres at Stora Karlsö of 20 – 50 m were similar to those recorded at other colonies (*e.g.* Camphuysen 2005, Hedd et al. 2009; Thaxter et al. 2009). As were dive efficiency values (Hedd et al. 2009, Thaxter et al. 2010). A steep increase in PDI for dive durations over 150 s adds support to the proposition of a 'behavioural aerobic dive limit' at this point for common murres (Tremblay et al. 2003, also Fig. 4B in Thaxter et al. 2010) that was also found in thick-billed murres (Croll et al. 1992); this may represent the actual aerobic dive limit (Hansen & Ricklefs 2004).

Daily activity patterns

We found a strong diel activity pattern, in agreement with many other studies of alcids and of observational studies of chick provisioning at this colony (Österblom & Olsson 2002). Like razorbills (*Alca torda*) in the southern Baltic Sea (Benvenuti et al. 2001), the common murres at Stora Karlsö followed a bimodal foraging strategy with longer duration overnight trips and shorter daytime trips. This pattern is likely to reflect the most profitable foraging times (around dusk and dawn) when diving activity was greatest and diving depths were rather shallow. This pattern was also found in several other studies for breeding (Camphuysen 2005, Regular et al. 2010) and post-breeding murres (Nevins 2004). This pattern probably reflects a balance between prey being accessible near the water surface and the time when sufficient light is available for visual foraging (Regular et al. 2010, Regular et al. 2011). The primary prey species for murres at Stora Karlsö, sprat, is known to perform a diel migration (Cardinale et al. 2003), moving to surface waters at night.

Foraging conditions

The use of longer trips in addition to short trips, radial pattern of trip paths, and the presence of diving towards the most distant part of these trips supports the proposition that prey closer to the colony could be depleted, favouring more distant foraging sites. However, the use of a limited sector of the sea suggests prey may not be widely dispersed but aggregated. However, this may also reflect a preference for flights in headwinds and tailwinds (see above). Stora Karlsö murres performed slightly fewer dives per dive bout and per foraging trip, suggesting higher prey availability. This may indicate little competition between fisheries and murres in this part of the Baltic Sea in 2009. It may also explain the stable or growing population at this breeding colony (Kadin et al. 2012) in contrast to other colonies of the species, *e.g.* around the North (JNCC 2011) and Norwegian Seas (Barrett *et al.* 2006) which have been decreasing in size. Further information about other sprat-dependent species is necessary to fully understand interactions between seabirds and the sprat fishery.

Conclusions

The combined use of separate GPS and TDR devices provides detailed behavioural data, which contribute novel information on individual alcid foraging decisions. The foraging trips for chick rearing common murre breeding at Stora Karlsö typically start with a short splashdown period followed by several, often spatially separated diving bouts. These diving bouts were interspersed with periods of surface activity and short flights. After the final diving bout, which typically occurred at the greatest distance from the breeding colony, birds usually returned directly to the breeding-ledge. During the study period, outward flights were significantly faster than inward flights, probably due to tailwind assistance. The murres appear to select either headwinds or tailwinds, avoiding crosswinds, and this may affect foraging locations chosen. However, to confirm these observations, studies under more variable wind conditions are required. There was a strong temporal pattern in foraging activity, with an apparent bimodal foraging strategy of long overnight trips, and short daytime trips. Diving frequency was greatest in the evening and dawn when diving depths were least.The present study illustrates how detailed information about foraging behaviour can be used to assess locations and activities where the interests of humans and birds overlap. Additionally the use of a relatively small marine area could be of interest with a view to setting up a marine protected area, protecting the population from future potential fishing conflicts and commercial shipping operating nearby.

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Tables

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

a: 4 individuals, 22 trips; b: 3 individuals, 18 trips; c: 6 individuals, 26 trips; d: 6 individuals, 19 trips; e: 4 individuals, 16 trips.

Table 2. *Uria aalge.* Summary statistics for all flights (105 from 36 trips by 6 birds) during foraging trips of common murre at Stora Karlsö, Sweden (see fig. 6 for comparison of 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

Table 3. *Uria aalge*. Summary of dives and dive bout characteristics for chick-rearing common murres at Stora Karlsö, Sweden in 2009. Post-dive interval (PDI) based calculations 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]

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

Figures

Fig. 1.

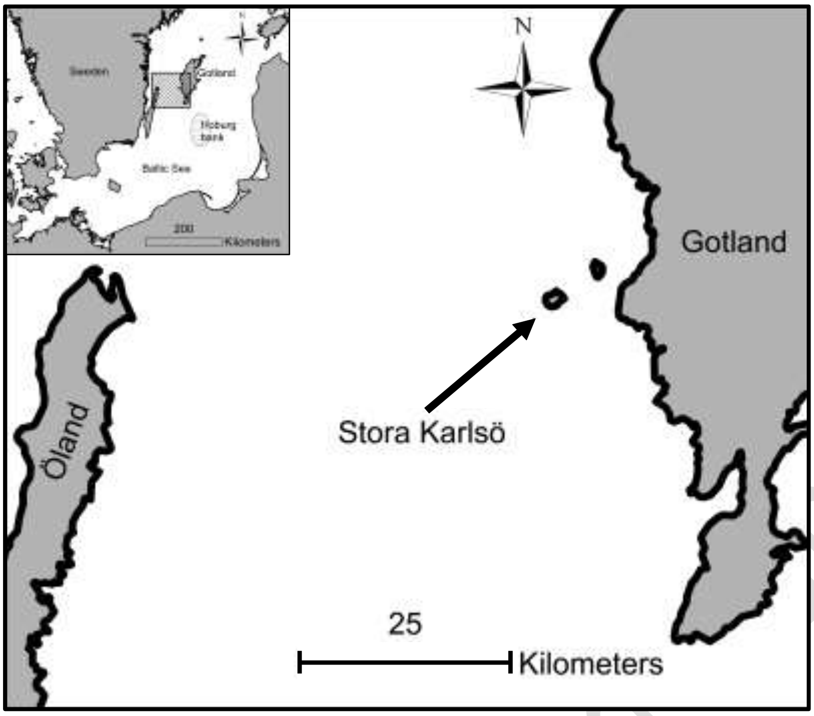

Fig. 2.

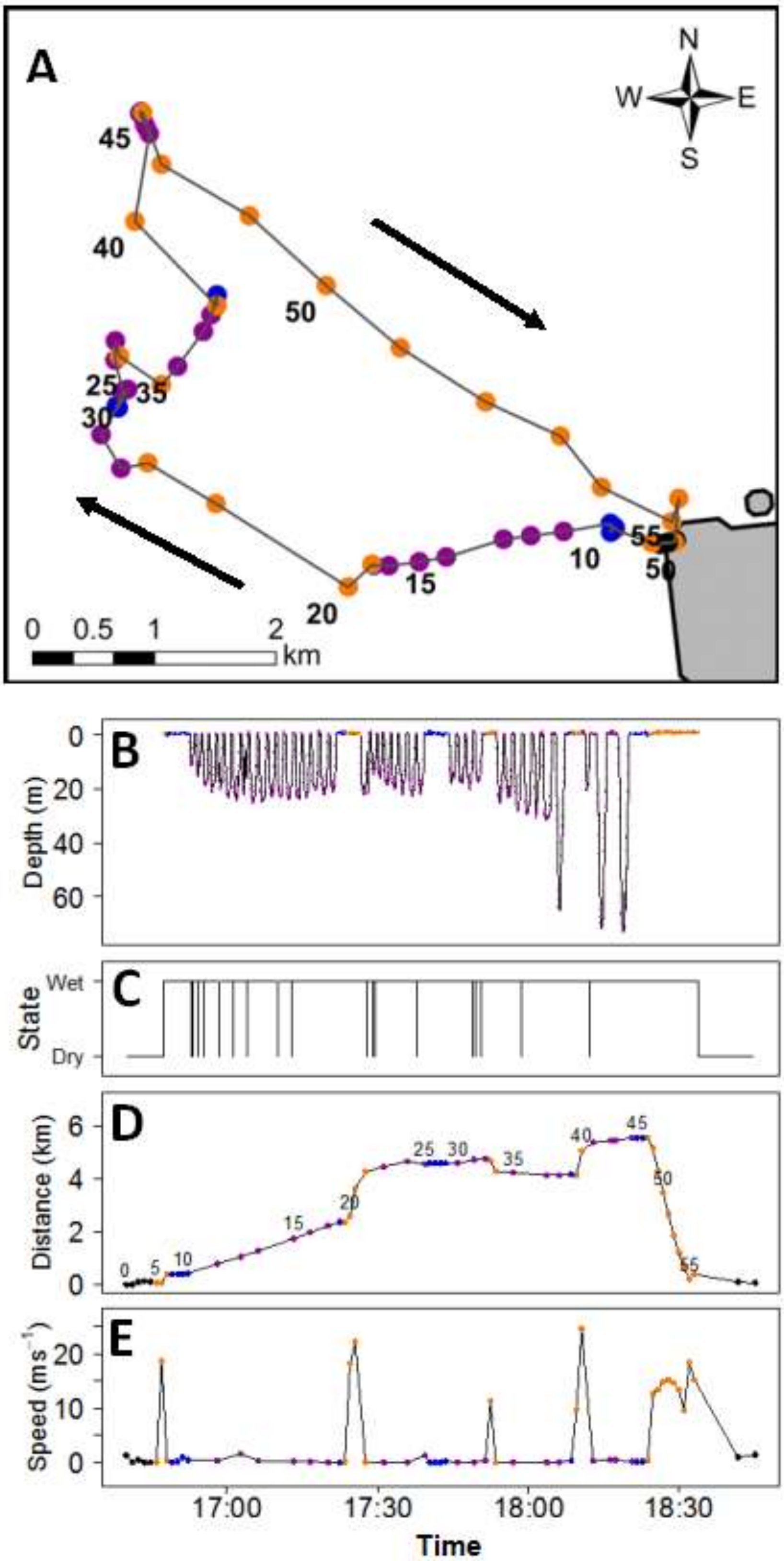
A
N
W
E
S
45
40
50
25
35
30
10
55
50
15
20
0
0.5
1
2
km
B
Depth (m)
0
20
40
60
C
State
Wet
Dry
D
Distance (km)
0
2
4
6
0
5
10
15
20
25
30
35
40
45
50
55
E
Speed (ms^{-1})
0
10
20
17:00
17:30
18:00
18:30
Time

Fig. 3.

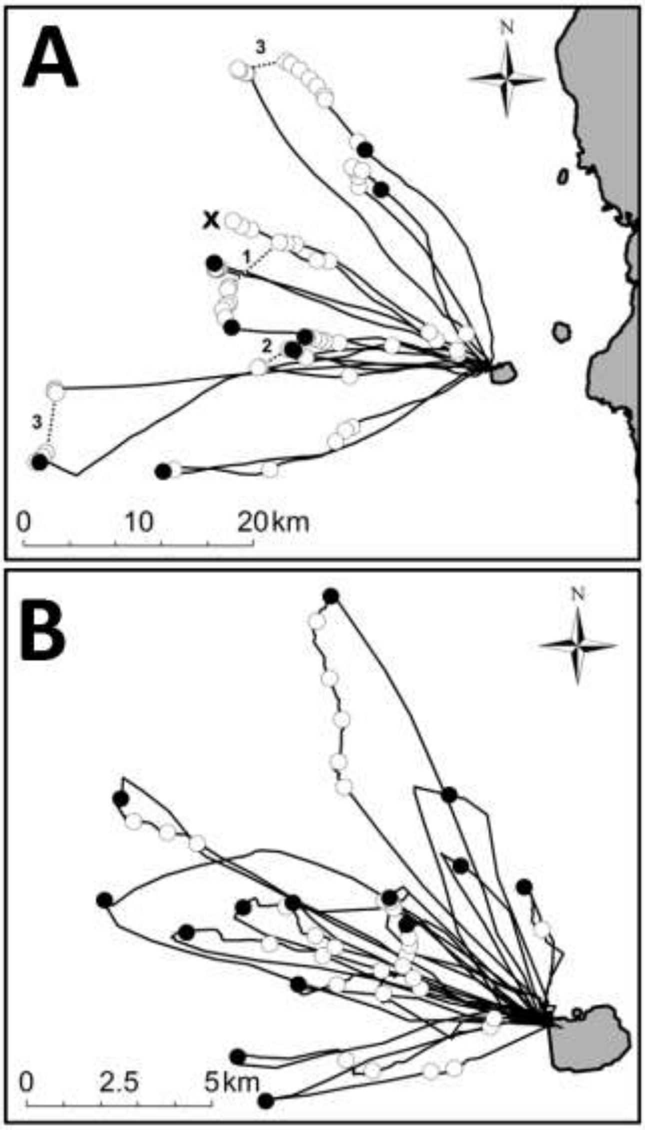

Fig. 4.

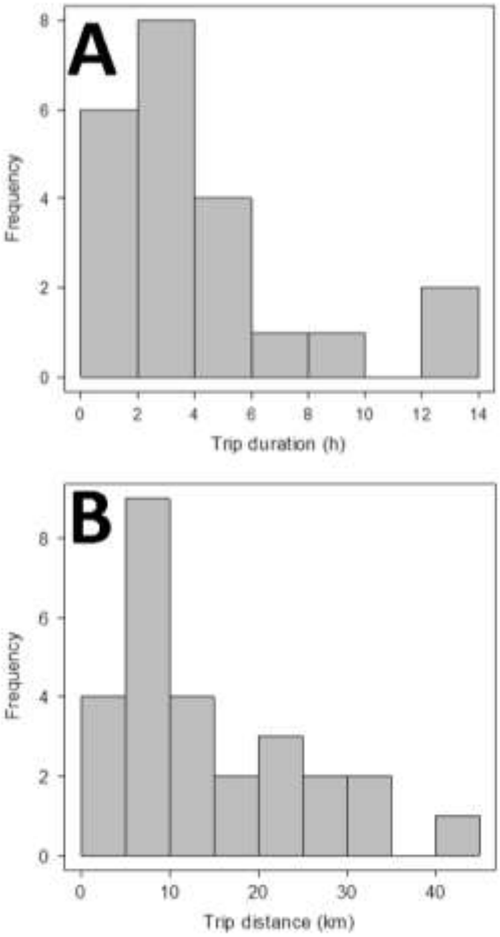
A
Frequency
0
2
4
6
8
0
2
4
6
8
10
12
14
Trip duration (h)
B
Frequency
0
2
4
6
8
0
10
20
30
40
Trip distance (km)

Fig. 5.

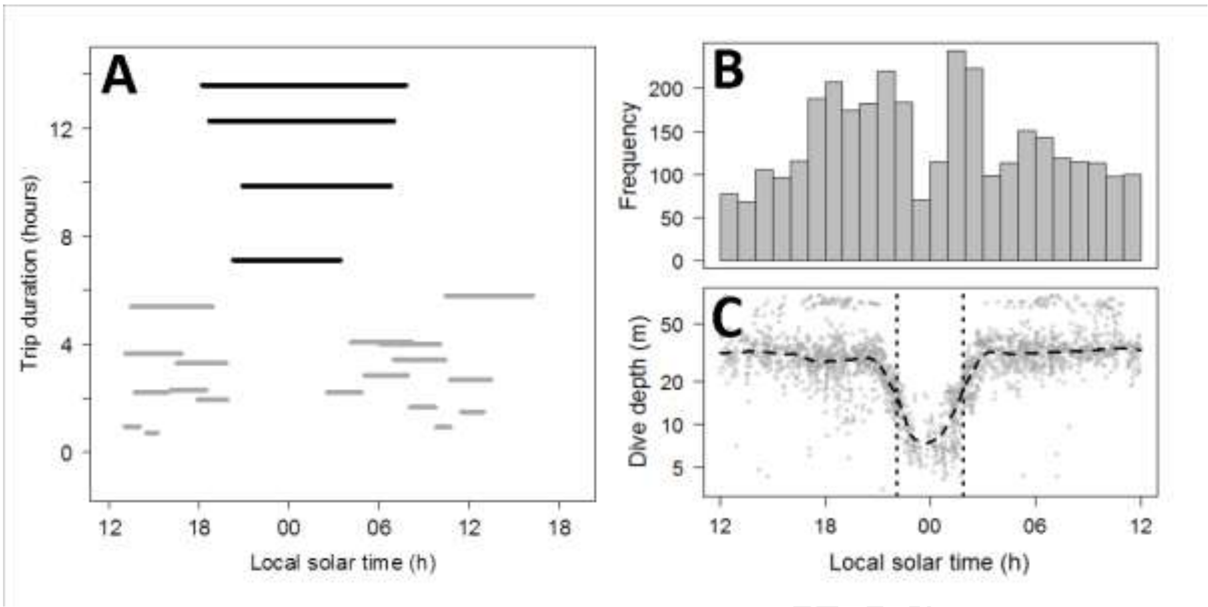
A
Trip duration (hours)
0
4
8
12
12
18
00
06
12
18
Local solar time (h)
B
Frequency
0
50
100
150
200
C
Dive depth (m)
5
10
20
50
12
18
00
06
12
Local solar time (h)

Fig. 6.

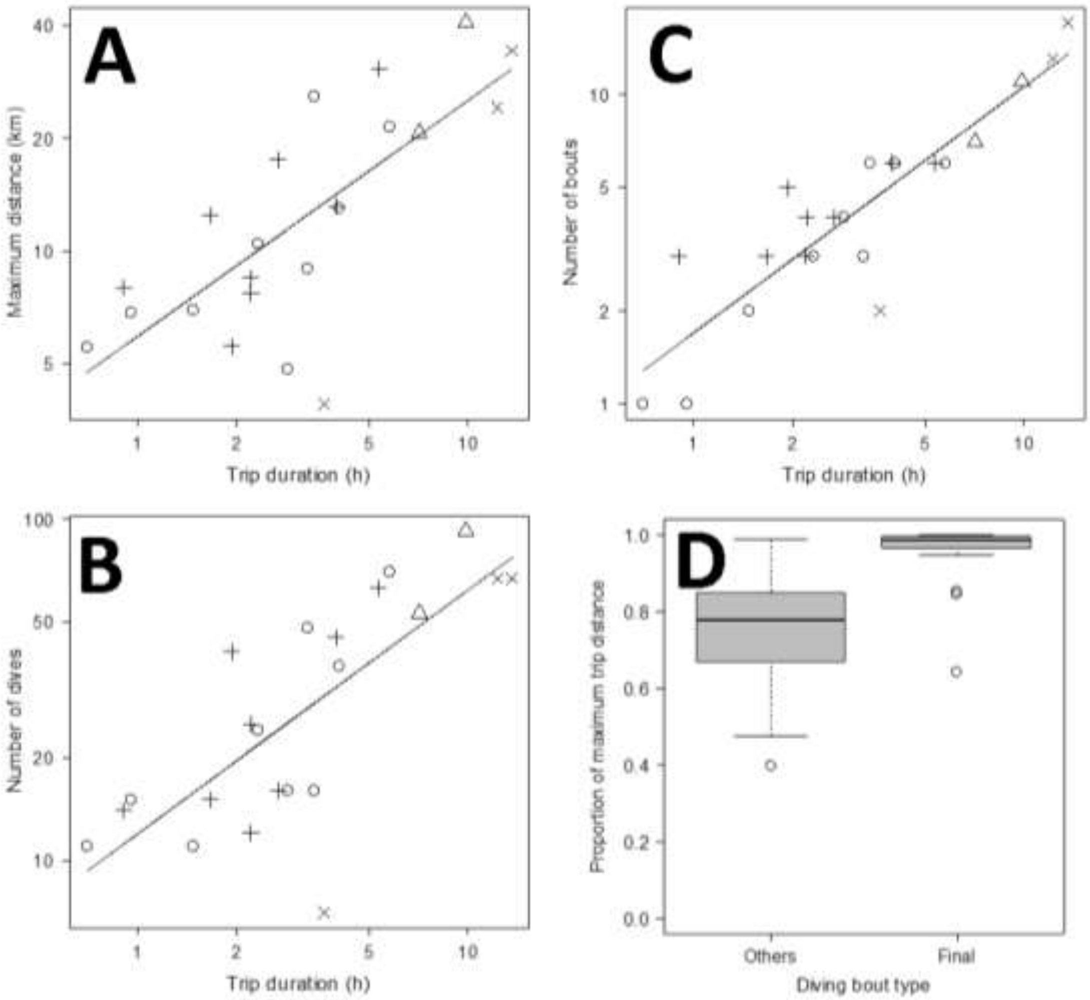
A
Maximum distance (km)
40
20
10
5
Trip duration (h)
1
2
5
10
C
Number of bouts
10
5
2
1
Trip duration (h)
1
2
5
10
B
Number of dives
100
50
20
10
Trip duration (h)
1
2
5
10
D
Proportion of maximum trip distance
1.0
0.8
0.6
0.4
0.2
0.0
Others
Final
Diving bout type

Fig. 7.

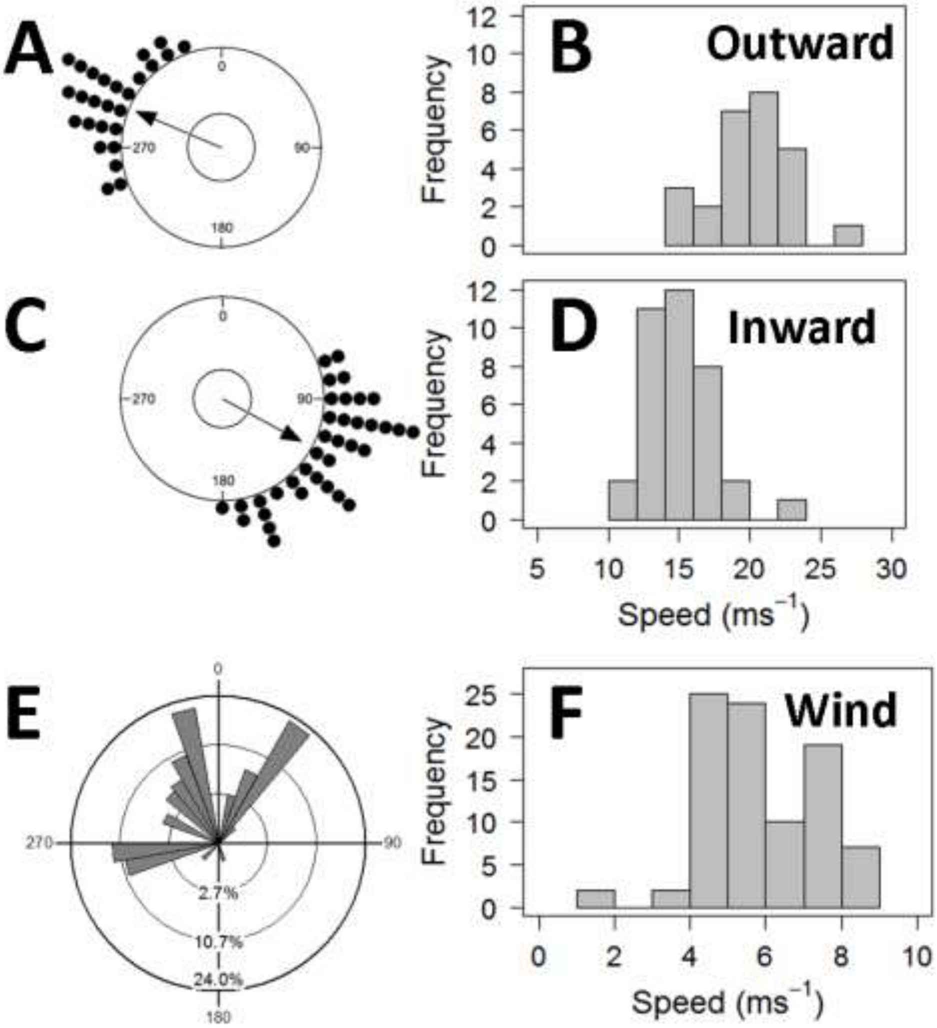
A
0
90
180
270
B
Outward
Frequency
0
2
4
6
8
10
12
C
0
90
180
270
D
Inward
Frequency
0
2
4
6
8
10
12
5
10
15
20
25
30
Speed (ms^{-1})
E
0
90
180
270
2.7%
10.7%
24.0%
F
Wind
Frequency
0
5
10
15
20
25
0
2
4
6
8
10
Speed (ms^{-1})

Fig. 8.

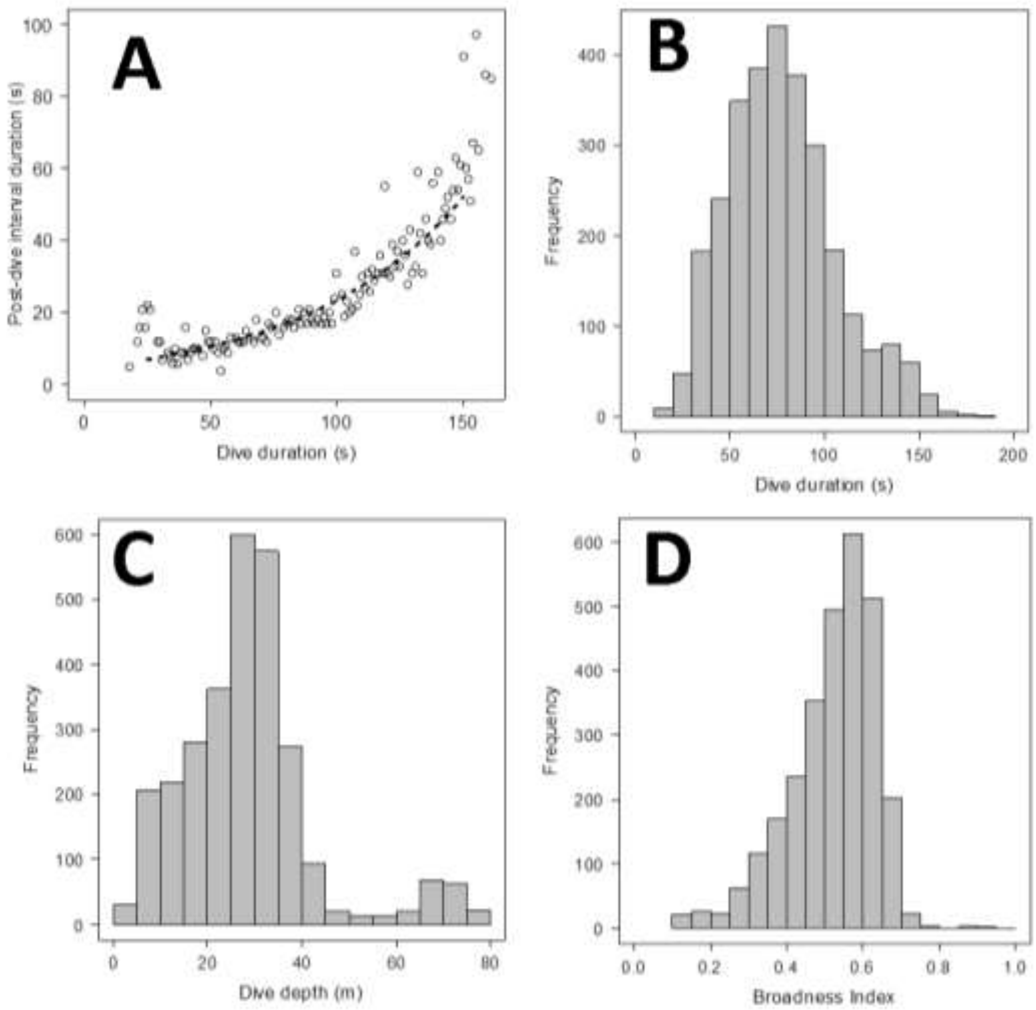
A
Post-dive interval duration (s)
0
20
40
60
80
100
Dive duration (s)
0
50
100
150
B
Frequency
0
100
200
300
400
Dive duration (s)
0
50
100
150
200
C
Frequency
0
100
200
300
400
500
600
Dive depth (m)
0
20
40
60
80
D
Frequency
0
100
200
300
400
500
600
Broadness Index
0.0
0.2
0.4
0.6
0.8
1.0

Figure legends

Fig. 1. Location of the study colony at the island of Stora Karlsö to the west of Gotland. Land is shaded. The main map is an expansion of the hatched area in the inset map.

Fig. 2. *Uria aalge. Example of a common murre foraging trip, GPS locations shown (A) and arrows to indicate travel direction, then various TDR and GPS parameters (B-E). The behaviour classification is indicated by colour throughout; flight (orange), diving bout (purple), water surface activity (blue), colony (black). GPS positions are numbered (A & C). B shows the depth reading from the TDR device, with dives visible as downward spikes. The wet-dry sensor has a lag phase, shortly before 18:30 the bird begins flying (E), but the sensor continues to show a 'wet' reading (C); only likely with a wet-dry transition. The distance from the island is indicated, D. Instantaneous GPS recorded speed (E), between c. 16:50 and 17:20 movement occurs (displacement from breeding-colony increases, D), this movement occurs during a diving bout, so is not reflected from the surface GPS records (E).*

Fig. 3. *Uria aalge.* All foraging trips of common murres tracked via GPS, split into long (A, maximum distance from breeding-ledge > 15 km) and short trips (B, maximum distance from breeding-ledge < 15 km). Dive bouts are indicated (open circles) and the final bout of a trip (closed circles). The coastline is indicated by the thick black lines, with land shaded. For four overnight trips (all long trips), there was a period (between 2300 and 0300 CEST) when the GPS devices were not recording, a dashed line is displayed for this period with a number indicating the number of diving bouts occurring during that time. One trip is truncated, due the depletion of the GPS battery (x in A).

Fig. 4. *Uria aalge.* Frequency histograms of common murre foraging trip duration (A, n = 22) and maximum distance (B, n = 27) from breeding ledge.

Fig. 5. *Uria aalge.* Foraging activity in common murres by time of day. Trip durations in common murres by trip start time (A) (n = 22), with overnight trips (black) and diurnal trips (grey) indicated. Frequency of dives in one hour bins (B) and depth (log axis) of dives (C, all individual dives shown by small grey open circles) with a smooth line fitted (LOWESS function in R, using 1 hour span). Local solar time (GMT + 1:10) displayed, with sunset and sunrise indicated by vertical dashed lines (C).

Fig. 6. *Uria aalge.* Foraging trips of common murres, scatter plots of relationship between foraging trip duration and activity (n = 22); maximum distance from breeding-ledge (A, linear regression, $t_{22} = 4.94$, $p < 0.0001$), number of dives (B, linear regression $t_{22} = 2.74$, $p < 0.0001$), and number of dive bouts (C, linear regression $t_{22} = 5.60$, $p < 0.0001$). Individuals are indicated by different symbols (open circle, cross, triangle, and x), linear regression lines (broken line) for log-transformed data, displayed with log axis. Box-and-whisker plot (D) comparing distance of final diving bouts to non-final dive bouts, using within trip ratio of dive bout distance to maximum distance from nest reached during trip, ends of whiskers represent the least and greatest values within 1.5 times the lowest or highest quartile (shown by box), values beyond whiskers are shown (open circles), medians at centre line. Final dives occur at significantly greater distances than earlier non final dives (paired t-test, $t = 4.47$, $n = 20$, $p < 0.001$).

Fig. 7. *Uria aalge.* Summary of resultant vector directions for common murre flights (A & C). The flights are split into outward (A & B) and inward (C & D) movements from the colony (see methods for definitions), with mean flight vector directions in 10° segments for each flight, mean vector shown (A; $\theta = 298.1°$, $r = 0.92$, $z = 22.13$, $p < 0.001$, $N = 26$. C; $\theta = 124.2°$, $r = 0.88$, $z = 27.82$, $p < 0.001$, $N = 36$). Flight speeds for outward flight (B, mean 20.0 ± 2.8 m s^{-1}) were greater than inward flight (D, mean 15.1 ± 2.5 m s^{-1}, paired t-test, $t = 3.14$, $df = 20$, $p = 0.005$). Circular plot (E) showing wind heading direction in 10° bins, and wind speed (F, mean 6.3 ± 1.6 m s^{-1}).

Fig. 8. *Uria aalge*. Relationship between post-dive interval duration (PDI) and dive duration in foraging common murres, with minimum PDI for dive durations at 1 s intervals (A), <150 s the relationship can be described by the regression line: $\mathrm{Log}_e(\mathrm{PDI}) = 0.015\,(\text{dive duration}) + 1.68$. Dive duration showed a near normal distribution with a slight right skew towards longer dives (B). Histogram of dive depths (C). The proportion of time spent at depth is indicated by the broadness index (D).

Supplementary material

S1

Detailed methods

Bird-borne data loggers

We used two different devices together: (1) a back-mounted GPSD, and (2) a leg-mounted TDR to record the foraging movements and diving behaviour.

(1) The GPSD was an unmodified commercial unit (model GT-120 by Mobile Action Technology, Inc. Taipei, Taiwan) which included a SiRF Star III Low Power chipset and 230 mAh battery. This was prepared for deployment by replacement of an outer housing with a heat-sealed plastic sleeve (HSP1-25.4/12.7-X, Hilltop Products Ltd, Warrington, UK; method after Guilford et al.2008), resulting in a cross-sectional area of 3 cm^2 (*cf.* Elliott et al. 2007). The precision of the GPSD was tested by placing on a windowsill in a building imitating poor signal conditions and ran for two days at 50 s intervals. 95 % of positions lay within 65 m latitude and 46 m longitude; 50 % of positions lay within 12 m latitude and 10 m longitude. Instantaneous ground speed recorded by GPSDs is very accurate, often within 0.1 m s^{-1} and a very high proportion within 1 m s^{-1} (*e.g.* Witte & Wilson 2004).

(2) TDRs were configured on a conditional logging mode to log pressure only when a salt water switch was on indicating submergence. Log intervals were set to 4 s for all but one device which was 5 s, providing sufficient resolution of dives usually of 30 to 120 s duration (*e.g.* Thaxter et al. 2009).

We attached TDRs to an aluminium ring (I.Ö. Mekaniska, Bankeryd, Sweden) mounted on the bird's left leg. GPSDs were attached dorsally along the midline over the bird's centre of gravity, minimising potential effects on balance (Ropert-Coudert et al. 2007). Black Tesa marine tape (product 4651 from Tesa SE, Hamburg, Germany) sealed with a small dab of cyanoacrylate glue, were used to attach devices to body feathers. After device attachment, *c.* 15 mins duration, birds were released near the ledge. When the common murres were released after the deployment, most flew out to sea a few hundred metres, landing on the water surface (TDR and observational data), and returned to the breeding-ledge (<15 mins). We recaptured the common murres after 2 - 10 days.

On average 4.5 ± 3.7 trips were tracked per an individual. This resulted in 3281 GPS positions from foraging trips. From these GPS tracked foraging trips we recorded 105 flights with a mean number of GPS fixes per flight of 5.6 ± 5.8. This comprised of 26 outward, 20 foraging, and 36 inward flights. The remainder of flights were not classified and were shorter non-foraging trips.

TDRs recorded for the complete deployment periods and averaged 4.6 ± 2.4 d (range 2.9 to 9.5 d) giving a total period of 765.5 h. 3326 dives were recorded from 7 individuals, 2866 excluding the tag with 50 m depth limit. In total 408 dive bouts were recorded, of which 120 had GPS positions, 23 being the final dive bouts of foraging trips.

Data treatment and statistics

Flight was classified as where GPS speeds >5 ms^{-1}, chosen as speed followed a bimodal distribution (Fig. S1). Flight durations were calculated as the length of time from the first to the final GPS fix where speeds exceeded 5 ms^{-1}. Then, to adjust for sampling interval, half the interval to the next fix and previous fix was added. Dive bouts were identified as described above. Surface resting was classified as any time that was not any of the other three behaviours. Time activity budgets were calculated as the mean proportion of time spent on each type of behaviour for each trip. GPS signals were impaired at the breeding ledge, due to the high cliff. Hence, recognition of trip start times used a combination of GPSD speed (identifying flight) and wet-dry data (for splashdowns).

Data from the GPSDs were mapped in ArcMap (9.3 and 10.0, Environmental Systems Research Institute, Redlands, CA), with which all map figures were produced. Data were initially analysed using the Hawth's Analysis Tools add-in (URL: http://www.spatialecology.com/htools), calculating the distance and bearing between GPS fixes, and the distance from the breeding-ledge. Dive bout positions were calculated from the mean of GPS locations during the bout period. Where no GPS locations were available, the closest (in time) GPS location was used, provided that it was <300 s before or after the bout, and that no large movement had occurred (>250 m between pre- and post-bout position) or birds were in flight.

Flight segments were separated from the GPS data, where a flight segment included consecutive fixes with speed over 5 ms^{-1} plus the position fix before and after this. For calculations based on speed, only the flight fixes were used; for those involving distance and bearing, the full flight segment was used. The mean speed is the mean of GPS recorded instantaneous ground speeds. Rhumb-line bearing and great circledistance were calculated between first and final position using functions ‘bearingRhumb’ and ‘distHaversine’ (Earth’s radius 6378137 m) from R package ‘geosphere’ (Hijmans et al. 2011).

We classified flights into three groups. (1) Outward flight, (2) foraging flights, and (3) inward flights. For outward and inward flights we calculate mean speeds and directions which were tested for uniformity with the Rayleigh test (Batschelet 1981). Outward and inward flight speeds were compared for each trip using a paired t-test. The summary for wind conditions provided here (Fig. 6 E & F and text) is for the mean of the conditions experienced for all GPS fixes obtained during flight.

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S2

Device effects

To assess device effects on study birds, we (1) compared the breeding success of tracked birds with neighbouring untracked pairs and (2) compared the bird weights before and following device deployment.

Method. (1) Throughout the study period, daily observations were made of all pairs breeding on the study ledge to determine the presence of a chick and continuation of breeding. From this the minimum chick age at fledging was calculated (observations began after hatching). Study pairs and control pairs (those not tracked) were compared statistically using Welch's two sample t-test with data checked for normality by Shapiro-Wilk test. (2) At capture (n = 9) and recapture (not all birds were weighed, n = 4) we weighed the murres to ± 5 g using a 1 kg Pesola® spring balance

Results. (1) The mean minimum chick age at first absence was not significantly different between study (mean = 12.9 ± 3.0 d , n = 9) and control (mean = 12.2 ± 3.0 d , n = 37) pairs (Welch's Two Sample t-test, t = 0.55, p = 0.59, df = 11.7) suggesting that fledging success was unaffected.

(2) The mean body mass at deployment for all individuals was 921 ± 62 g (n = 9). For four birds for which re-capture weight was also recorded the start weight was 889 ± 73 g and the end weight 869 ± 28 g. The rate of weight change was -12 g d^{-1}, although one bird gained weight (16 g d^{-1}), the other three lost weight (-21 ± 11 g d^{-1}).

Interpretation

Breeding success did not differ between study and control birds. However weight losses were recorded although these were similar to those reported in other studies using biologgers (*e.g.* Benvenuti et al. 2001, Paredes et al. 2008), and this may reflect normal adaptive weight loss (Elliott et al. 2008, Jacobs et al. 2011). Similar device weights were not found to affect dive behaviour (Camphuysen 2005) in a comparison of murres carrying either a 5 g or 23 g, though flight behaviour could be affected (Vandenabeele et al. 2011).

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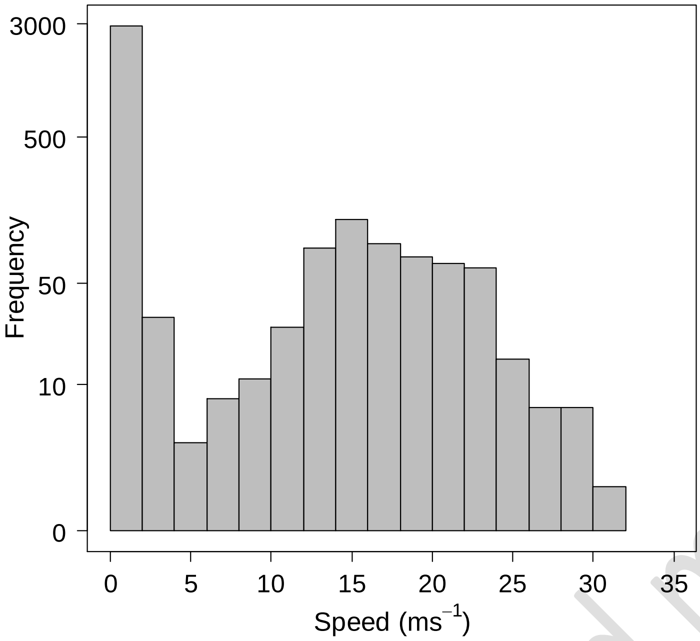
Figure S1



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