



Foraging behaviour of sympatric razorbills and puffins

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ABSTRACT: Many marine predators coexist at colonies, creating a zone where there could be significant inter- and intraspecific competition. To minimize the potential for direct competition, under the principle of competitive exclusion, sympatric predators may differ in their foraging behaviour at the colony. At Skomer, Wales, razorbills *Alca torda* and puffins *Fratercula arctica* both breed at the same time of year, forage on sand eels *Ammodytes* sp. and their populations are stable or declining, meaning that they may be close to carrying capacity and experiencing competition. To examine how they differ in their foraging behaviour, time-depth-temperature recorders were attached to the legs of chick-rearing individuals of both species. Puffins have lower wing-loading and lower total oxygen stores than razorbills and are therefore expected to invest more time in flying and less time in diving than razorbills. Mean (± 1 SE) dive depth was 11.8 ± 0.45 m for puffins and 8.2 ± 0.21 m for razorbills, while mean dive duration was 40 ± 0.45 s for puffins and 24 ± 0.21 s for razorbills. Both species spent most of their dive time making shallow, V-shaped dives during daylight hours. In contrast to our prediction, foraging behaviour was very similar between the 2 species, although puffins tended to spend more time both diving and flying. The higher diving and flying rates of puffins may be associated with multiple prey loading, as puffins tend to bring back smaller (and therefore more) prey items than do razorbills.

KEY WORDS: Diving behavior · Auks · Bio-logging · Alcids

INTRODUCTION

The principle of competitive exclusion, a basic tenet of ecology, states that complete competitors cannot coexist (Gauze 1934, Hutchinson 1959, Schoener 1974). That is, the n-dimensional niche hyper-volume between any 2 sympatric (and therefore competing) species must differ (MacArthur 1958, Hutchinson 1959, Pianka 1969, Wilson 2010). Nonetheless, many seabird and marine mammal colonies are characterized by several co-existing species with apparently similar dietary niches (Diamond 1978, Croxall & Prince 1980, Gaston 2004). Competition is likely strongest during the reproductive period because all individuals are constrained to feed within a limited

radius of the central place and cannot wander entire oceans searching for an optimal foraging patch (Ashmole 1963, Gaston et al. 2007). Many cliff- or burrow-nesting seabirds are apparently not limited by nest-sites, and competition must occur at sea (Elliott et al. 2009b, Masello et al. 2010, Wakefield et al. 2013), presumably leading to differences in their foraging niches over evolutionary time. In support of this theory, sympatric seabird species often have different foraging strategies (Ishtiaq et al. 2010, Barger & Kitaysky 2012; Table 1).

In northern oceans, several auk species coexist at many colonies and apparently utilize different foraging strategies (Gaston 2004, Elliott et al. 2010b, Thaxter et al. 2010). For instance, common guillemots *Uria*

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Table 1. Summary of studies that have directly investigated differences in the foraging behaviour of seabirds feeding on similar prey

Common name	Taxon	Foraging behaviour	Source
Macaroni penguin Gentoo penguin	<i>Eudyptes chrysolophus</i> <i>Pygoscelis papua</i>	Macaroni penguins dived more and were more efficient at shallow depths	Mori & Boyd (2004)
Humboldt penguin Magellanic penguin	<i>Spheniscus humboldti</i> <i>S. magellanicus</i>	Variation between species in foraging range and dive depth was greater than between sexes, with Magellanic diving deeper	Raya Rey et al. (2013)
Adélie penguin Chinstrap penguin Gentoo penguin	<i>P. adeliae</i> <i>P. antarctica</i> <i>P. papua</i>	Gentoo are inshore, deep divers; the other 2 are offshore, shallow divers. Furthermore, Adélie finish chick-rearing as chinstraps begin to crèche	Trivelpiece et al. (1987)
Adélie penguin Chinstrap penguin Gentoo penguin	<i>P. adeliae</i> <i>P. antarctica</i> <i>P. papua</i>	<10% overall (horizontal and vertical) overlap between species. Adélie were most efficient at shallow depths, chinstraps at intermediate depths and gentoo at deep depths, and each species foraged primarily where they were most efficient	Wilson (2010)
Rockhopper penguin Gentoo penguin Magellanic penguin	<i>E. chrysochome</i> <i>P. papua</i> <i>S. magellanicus</i>	<20% overall horizontal overlap between species, with additional segregation in dive depth and time of day. Strong horizontal segregation between colonies from the same species	Masello et al. (2010)
Scopoli's shearwater Cory's shearwater	<i>Calonectris diomedea</i> <i>C. borealis</i>	During chick-rearing, but not incubation, foraging ranges largely do not overlap	Afan et al. (2014)
Common diving petrel South Georgia diving petrel Blue petrel Antarctic prion	<i>Pelecanoïdes urinatrix</i> <i>P. georgicus</i> <i>Halobaena caerulea</i> <i>Pachyptila desolata</i>	Blue petrels forage primarily at night, while Antarctic prions forage during the day; no difference in diving behaviour. Both diving petrels dive deeper, with commons diving more often but for shorter duration	Navarro et al. (2013)
Wandering albatross Black-browed albatross Grey-headed albatross	<i>Diomedea exulans</i> <i>D. melanophris</i> <i>D. chrysostrama</i>	Strong spatial segregation in the foraging area of the 3 species, except in an area where high trawler traffic increases food abundance	Weimerskirch et al. (1988)
Red-legged cormorant Rock shag	<i>Phalacrocorax gaimardi</i> <i>P. magellanicus</i>	Almost complete segregation, with red-leggeds feeding closer to the colony than rocks; in isolation, rocks foraged closer to the colony than in sympatry	Frere et al. (2008)
Ancient murrelet Cassin's auklet	<i>Synthliboramphus antiquus</i> <i>Ptychoramphus aleuticus</i>	Although smaller, auklets have higher oxygen stores and therefore dive deeper, more often and with a longer bottom time	Elliott et al. (2010b)
Common guillemot Razorbill	<i>Uria aalge</i> <i>Alca torda</i>	Guillemots had higher wing-loadings and oxygen stores, flew less, dived longer and spent more time at the bottom of their dives	Paredes et al. (2008), Thaxter et al. (2010)
Common guillemot Brünnich's guillemot Razorbill	<i>U. aalge</i> <i>U. lomvia</i> <i>A. torda</i>	Overlap in foraging area during the breeding season, but razorbills winter farther south. Overlap in dive depth during the breeding season between guillemots, but razorbills dive shallower	Linnebjerg et al. (2013)
Atlantic puffin Razorbill	<i>Fratercula arctica</i> <i>A. torda</i>	Puffins dived slightly longer than razorbills and tended to spend more time diving and flying	This study

aalge have higher total oxygen stores and proportionately smaller wings and are more efficient at diving than razorbills *Alca torda*; guillemots dive deeper with longer bottom times (Paredes et al. 2008, Thaxter et al. 2010). Thus, although both species feed predominately on sand eels *Ammodytes* sp. in the North Sea, guillemots exploit sand eels at deeper depths than razorbills (Thaxter et al. 2010). Atlantic puffins *Fratercula arctica* are a third species of auk that is often sympatric with both razorbills and guillemots and also predominately feeds its chick with sand eels and sprats *Sprattus* sp. (Harris & Wanless 2012). Both puffins and razorbills have similar mass-specific oxygen stores (Table 2), but puffins (~420 g) are lighter than razorbills (~600 g), so their dive capabilities are likely to be lower due to higher mass-specific oxygen consumption rate (Watanuki & Burger 1999). Likewise, because razorbills have 55% greater wing-loading than puffins (Table 2), razorbills may spend more time diving and less time flying than puffins (Thaxter et al. 2010). Whereas guillemots can carry only a single, large sprat back to their young, razorbills provision their young with 2 to 10 smaller sand eels, and puffins carry up to 50 small sand eels back to their young (Harris & Wanless 2012).

The dive behaviour of puffins has been reported with non-electronic recording devices such as capillary tubes, which only provide a single maximum depth value, and only 2 recent studies have reported puffin dive behaviour with electronic recordings (e.g. Harris & Wanless 2012). The purpose of this study was 2-fold: (1) to document the diving behavior of chick-rearing puffins; and (2) to determine how puffins' foraging behaviour might differ from sympatric razorbills. We studied the birds during the mutual chick-rearing period because this is when the birds are likely to be particularly constrained by sympatric competition due to the higher energy costs of chick-provisioning (Hansen 2003, Elliott et al. 2014).

MATERIALS AND METHODS

Study populations

Our study was carried out at a razorbill *Alca torda* colony (The Basin) and a puffin *Fratercula arctica* colony (North Haven) on Skomer Island (51°44'N,

Table 2. Differences in the 3 species of auks feeding on sand eels. Sources: ^aHarris & Wanless (2012), ^bElliott et al. (2013), ^cHansen (2003)

	Body mass ^{a,b} (g)	Oxygen stores ^{b,c} (ml O ₂ kg ⁻¹)	Wing-loading ^b (N m ⁻²)	Number of fish delivered ^a	Fish size ^a
Guillemot	1000	51	205	1	Large
Razorbill	600	57.2	167	2–10	Medium
Puffin	420	57.8	108	Up to 50	Small

5° 19' W), Wales, UK. On Skomer Island, the population size of razorbills is ~6500 individuals and that of puffins is ~19 000 individuals (Büche et al. 2013). Individuals were selected from certain locations for both species to avoid potential effects of the nesting locations on diving behaviour. The fledging strategy differs between the 2 species, with puffins being fully altricial (young go to sea near adult size after ~44 d in the nest) and razorbills being intermediate (young go to sea at ~30% of adult size after ~20 d in the nest). We attached time-depth-temperature recorders (TDRs) to 8 razorbills on 21 June to 3 July 2013 and to 12 Atlantic puffins on 22 to 28 June 2013. Data were recorded for up to 3 d (puffins) or 7 d (razorbills), and the devices were recovered after 3 d (puffins) and 7 d (razorbills).

Device attachment

Devices were attached to the leg bands of parental birds with young chicks. For the razorbills, we attached CEFAS loggers (Cefas G5, Cefas Technology) that recorded pressure every second and temperature every 15 s for up to 7 d (mass = 2.7 g; diameter = 1 cm; length = 3.3 cm), alongside a 12 g GPS logger (unpacked i-gotU GT-120: Mobile Action, Taiwan; mass = 12 g; length = 43 mm; width = 24 mm; height = 9 mm). GPS loggers were sealed in heat-shrink plastic and attached dorsally using tesa marine cloth tape underlying a small number of contour feathers (Shoji et al. 2014). The total mass of devices with attachment materials in each deployment was ~19 g (always <4.0% of adult body mass, see Phillips et al. 2003, Vandenabeele et al. 2012; device attachments naturally fall off within 3 wk as a failsafe; Shoji et al. 2014). Because previous studies had shown that puffins were particularly susceptible to nest desertion (Wanless et al. 1990, Gaston 2004, Whidden et al. 2007, Harris & Wanless 2012), we (1) worked exclusively with puffins with young chicks and (2) attached smaller Lotek 1900

TDRs (LAT 1900, Lotek Wireless) that recorded pressure every 4 s and temperature every 15 s for roughly 1 d (mass = 2.0 g; length = 17 mm; width = 9 mm; height = 16 mm). We extracted dive depth, dive duration and surface interval duration for each dive after accounting for device drift (Elliott & Gaston 2009). We used the sequential differences method to subdivide dives into bouts using surface intervals (difference criterion: 51 s for puffins; 60 s for razorbills; Mori et al. 2001). We considered surface interval as a function of dive depth because surface intervals correlated slightly better with dive depth than dive duration (razorbills: $R^2 = 0.116$ vs. 0.132 ; puffins: $R^2 = 0.343$ vs. 0.405), as is the case for closely-related guillemots (Elliott et al. 2008), because substantial energy during the dive is used overcoming buoyancy to descend to depth (Watanuki et al. 2003, Lovvorn et al. 2004). We classified dive shape as V-, U- or W-shaped (Elliott et al. 2008).

We used the temperature log to determine when the bird was flying (Elliott et al. 2009b, Linnebjerg et al. 2014). Leg tucks, which occurred primarily at night, were distinguished by the rapid rise to high temperature (Robertson et al. 2012). As recommended by Linnebjerg et al. (2014), we simultaneously attached GPS loggers (i-gotU) to razorbills that recorded location every 15 min to validate our estimates of flight time. As our interpretation of the temperature log agreed with the GPS log >98% of the time, we were confident in our ability to record flight times for both razorbills and puffins using temperature logs alone.

Statistical analysis

We used general linear mixed models (GLMM) with individual as a random factor to compare foraging behaviour between razorbills and puffins. We considered species and dive depth, duration and frequency of dives as a function of time of day (circularly transformed by $\cos[2\pi \times \text{hours since solar midnight}]$ to provide a cycle that is in phase with light level). We included circularly transformed time of day as a covariate because light levels are known to strongly impact the dive behavior of many animals (e.g. McMahon & Holanov 1995, White et al. 2007, Zimmer et al. 2008), including auks (Croll et al. 1992, Paredes et al. 2008, Regular et al. 2011). Prior to the analyses, we assessed the effect of time of day and individual identity on dive duration and dive depth by species judged by Akaike's information criterion

(AIC) (Burnham & Anderson 2002). Both time of day (dive duration: $\Delta\text{AIC} = 1058$, dive depth: $\Delta\text{AIC} = 899$) and individual identity (dive duration: $\Delta\text{AIC} = 2539$, dive depth: $\Delta\text{AIC} = 2400$) increased the parsimony of models for dive depth and duration. Thus, we included time of day as a fixed effect and individual identity as a random effect in these models. We also considered surface interval duration and dive duration as a function of dive depth. Finally, we completed a principal component analysis to examine how puffins and razorbills differed in their use of different foraging behaviours. We only included axes with eigenvalues > 1.0. We used R 3.0.3 (R Development Core Team 2011) for all analyses.

RESULTS

We retrieved TDRs from 7 puffins *Fratercula arctica* and 7 razorbills *Alca torda*. All un-retrieved birds were spotted in the colony after deployment, but we failed to recapture them. No difference was found in breeding success between our study birds and control birds that are part of the long-term study run by the Edward Grey Institute at the University of Oxford. In total, we recorded 15 383 dives from razorbills ($n = 7$ birds) and 3414 dives from puffins ($n = 7$ birds). Dive duration was longer ($t_{12} = -3.17$, $p = 0.008$, GLMM with individual as random effect and time of day: $\cos[2\pi \times \text{hours since solar midnight}]$ as a fixed effect) and dive depth tended to be deeper ($t_{12} = -1.90$, $p = 0.08$) for puffins than razorbills (Table 3, Fig. 1). Dive duration was longer ($t_{12} = -4.32$, $p = 0.001$, GLMM with individual as random effect and depth as a fixed effect) and surface interval tended to be shorter for puffins than for razorbills for a given dive depth ($t_{12} = 2.14$, $p = 0.05$, Fig. 1). More than 95% of dives were V-shaped for both species. Puffins spent $5.7 \pm 3.3\%$ of the day flying with average flight duration of 7.47 ± 2.91 min, while razorbills spent $4.9 \pm 1.4\%$ of the day flying with average flight duration of 6.45 ± 1.20 min. Including species (razorbill/puffin) did not increase the parsimony for models explaining flight duration ($\Delta\text{AIC} = 1.0$). The first 3 principal components (PC) explained >77% of the overall variance, and no other axis explained >10% of the variance (Table 4). Dive depth and number of flights per day loaded heavily and negatively on the first axis, while percentage of time diving loaded heavily and positively on the second axis (Table 5). Razorbills tended to be associated with a positive first PC axis score, while puffins tended to be associated with a positive second PC axis score.

Table 3. Dive parameters for Atlantic puffins and razorbills breeding on Skomer, including all dives >2.5 m in depth. Values are (where applicable) mean ± SD

Individual	Depth (m)	Duration (s)	Max. depth (m)	Max. duration (s)	No. of dives per day	No. of dives per bout	Bout length (s)
Atlantic puffins							
515	15.7 ± 12.6	52.2 ± 29.9	47.6	123.1	310	19.6 ± 21.2	1320 ± 1368
200	9.8 ± 7.4	33.2 ± 19.8	33.7	90.5	460	25.0 ± 18.1	1023 ± 717
152	5.9 ± 3.4	28.0 ± 16.4	23.5	93.7	600	26.6 ± 18.6	1105 ± 817
1	7.5 ± 5.9	27.9 ± 19.7	23.9	82.7	416	43.6 ± 28.7	1587 ± 1524
523	13.8 ± 11.2	42.6 ± 25.6	37.6	95.5	510	23.6 ± 16.8	1320 ± 771
518	12.8 ± 13.5	36.6 ± 27.9	46.4	116.6	283	25.6 ± 26.1	1321 ± 871
148	9.7 ± 7.6	57.4 ± 25.4	39.4	105.8	283	11.6 ± 12.8	818 ± 904
Mean	11.8 ± 4.2	39.7 ± 11.6	36.0 ± 9.7	101.1 ± 14.6	409 ± 123	25.1 ± 20.3	1213 ± 996
Razorbills							
k24763	8.9 ± 6.4	26.1 ± 16.2	56	93	417	17.0 ± 22.1	651 ± 749
k24909	5.8 ± 3.7	22.4 ± 10.9	25.1	69.8	448	27.0 ± 33.2	776 ± 946
k93793	10.3 ± 5.0	31.1 ± 13.6	25.2	71.4	234	17.1 ± 25.4	839 ± 1172
m27931	8.6 ± 4.9	24.1 ± 12.8	26.5	68.2	295	20.0 ± 19.5	724 ± 703
m93896	8.2 ± 5.8	22.4 ± 16.0	29.3	64.8	362	14.3 ± 4.5	660 ± 208
m93998	6.6 ± 3.2	17.8 ± 10.3	21.6	52.3	511	19.2 ± 26.4	638 ± 759
m93924	8.8 ± 5.4	23.5 ± 16.1	31.3	73.4	511	26.3 ± 39.4	1052 ± 1288
Mean	8.2 ± 1.5	24.0 ± 4.1	30.7 ± 11.6	70.4 ± 12.1	397 ± 105	20.1 ± 24.4	763 ± 832

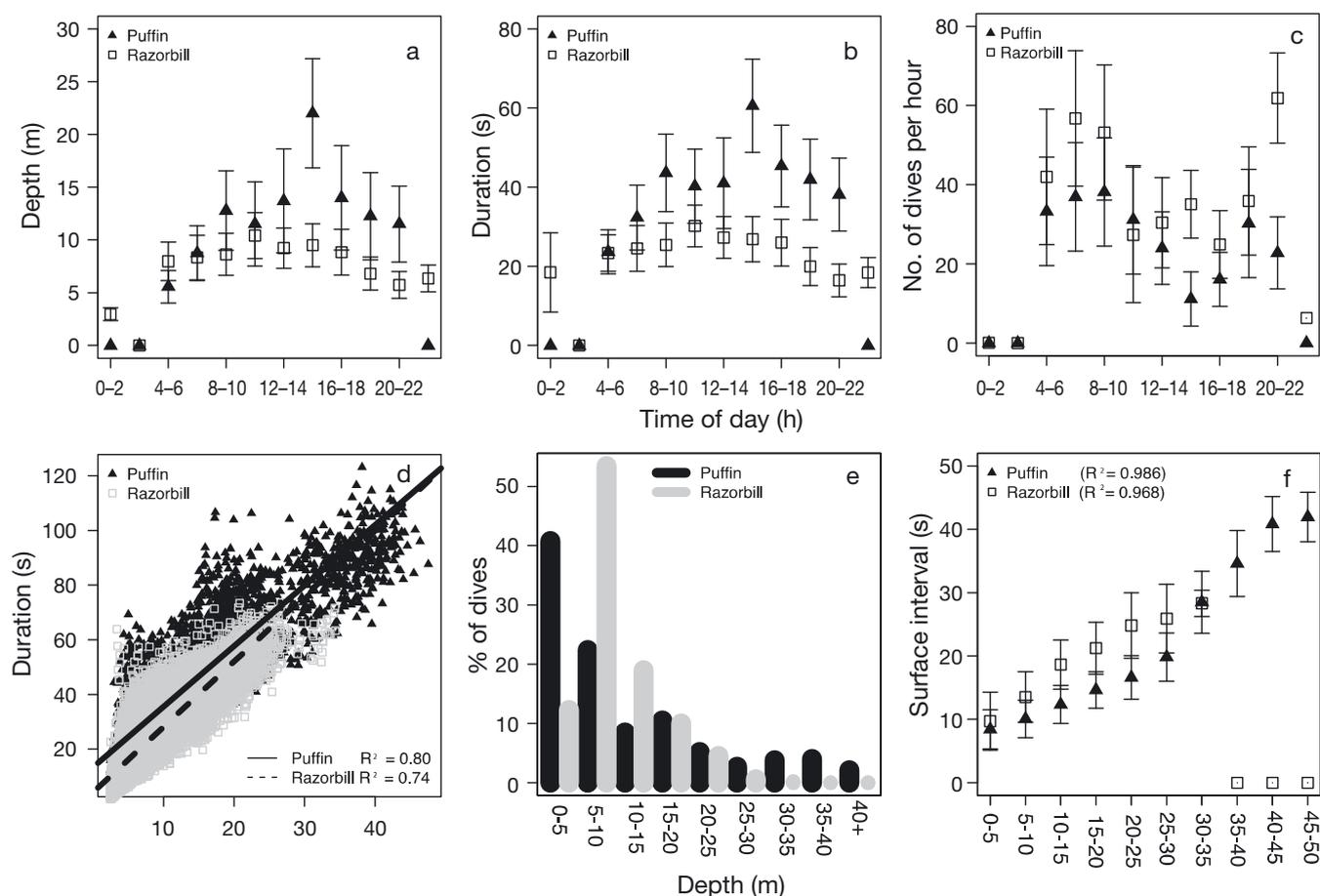


Fig. 1. Average (a) depth, (b) duration and (c) number of dives per hour relative to time of day, (d) dive duration relative to dive depth, (e) frequency of dives to different depths and (f) average surface interval duration relative to dive depth, for Atlantic puffins and razorbills

Table 4. Loadings for principal components analysis of dive behaviour based on average values for each individual. Loadings < 0.1 are not shown. The component with the highest loading is shown in **bold**

Variable	PC1	PC2	PC3
Percent of variance explained	32 %	25 %	20 %
Average dive depth	-0.490	0.211	-0.300
Maximum depth	-0.393	0.302	-0.257
Average surface interval duration	-0.282	-0.278	-0.127
Residual of dive duration on dive depth	0.375	0.429	-0.464
Number of dives per day		0.349	0.370
Percent time spent diving	0.131	0.656	
Number of flights per day	-0.480		0.441
Percent of time spent flying	-0.367	0.222	0.526

DISCUSSION

Puffin diving behaviour

Puffin *Fratercula arctica* dive behaviour was quite similar to other non-*Uria* auk species, consisting primarily of many shallow (~5 to 20 m) V-shaped dives during daylight hours. Not surprisingly, dive depth was apparently limited by visibility as dive depth was deeper during the middle of the day and no diving occurred at night (Croll et al. 1992, Regular et al. 2011). The number of dives per hour peaked in the morning and evening, which coincides with the peak in feeding rates of offspring by parental puffins at Skomer (Büche et al. 2013). Similar peaks in dive rates after dawn and before dusk were observed with puffins at the Isle of May (Wanless et al. 1990, Harris & Wanless 2012). We speculate that such a relationship reflects a need to provide food for the offspring before and after the nighttime fasting period and perhaps it requires more energy and/or investment to feed.

Puffin dive behaviour at Skomer was quite similar to the dive behaviour elsewhere (Table 1), although

dives were shallower than recorded in some cases by capillary tubes (capillary tubing, closed at one end and dusted with icing sugar, can be used to determine a single maximum depth over the course of deployment based on the maximum distance sea water extends into the tube and dissolves the icing sugar; Kooyman et al. 1971). Capillary tubes can be inaccurate even over short deployments, leading to erroneously deep maximum depths for a species (Elliott & Gaston 2009). Nonetheless, our maximum depth (48 m) was deeper than that recorded at our study site using capillary tubes (27 m;

Davidson 1994). Both maximum and average depth of puffins at Skomer was deeper than at Isle of May, perhaps because the bathymetry within the foraging range of the puffin is generally shallower at Isle of May than at Skomer (Fig. A1 in the Appendix). Average dive duration was slightly shorter and maximum duration was slightly longer than predicted based on allometric relationships across all auks (predicted average duration: 47 s; predicted maximum duration: 114 s; Watanuki & Burger 1999).

Puffins dived on average 409 times per day at Skomer compared with 1148 times per day at the Isle of May (Harris & Wanless 2012). Although average dive duration at Skomer was longer, the average hours per day submerged at the Isle of May (7.8 h) was higher than at Skomer (4.6 h). The discrepancy is partially explained by the timing of deployments, as the puffins observed at Isle of May included puffins with older offspring, which likely had higher energy demands necessitating more food and higher dive rates (Harris & Wanless 2012). If we assume that puffins need to capture 447 sand eels per day to feed their young and maintain their own body weight

Table 5. Dive behaviour of puffins as recorded at different locations and by different instruments. Average values of dive behaviour (maximum values in parentheses) are presented

Location	Depth	Duration	Instruments	Source
Isle of May, Britain	4 (20)	–	Time-depth recorder	Harris & Wanless (2012)
Isle of May, Britain	–	30 (114)	Radio telemetry	Wanless et al. (1988)
Isle of May, Britain	(33)	–	Capillary tube	Wanless et al. (1990)
Petit Manaan, Maine	–	9.7 (40.7)	Time-depth recorder	Spencer (2012)
Newfoundland	(60)	–	Fishing nets	Piatt & Nettleship (1985)
Newfoundland	(68)	–	Capillary tube	Burger & Simpson (1986)
Norway	(45)	–	Capillary tube	Barrett & Furness (1990)
Labrador	(41)	–	Capillary tube	Baillie (2001)
Skomer, Britain	(27)	–	Capillary tube	Davidson (1994)
Skomer, Britain	11.8 (47.6)	9.7 (40.7)	Time-depth recorder	Our study

(details in Harris & Wanless 2012), then, based on our data, puffins at Skomer likely catch just over 1 fish per dive, compared with <1 fish every other dive at the Isle of May.

At Skomer, most puffins apparently forage relatively close to the colony. Puffins averaged about 1.4 h d^{-1} flying. Assuming they flew at 19.2 km h^{-1} (based on the allometric equation $19.05M^{0.12}$ [M = body mass in kg] for auks, Fig. 4 in Elliott et al. [2004]) and always flew directly away from or directly toward the colony, this gives an average foraging range of 42 km. In reality, birds visit the colony multiple times per day to feed offspring, and likely move in different directions. The foraging range of 7.7 km, based on average flight duration (7.5 min), might be more typical. This coincides with the observation that 85% of puffins carrying fish were within 15 km of the Skomer colony and 99% were within 25 km (Stone et al. 1992). In contrast, at the Isle of May, 1 puffin spent 64% of its time within 2 km of the colony (Wanless et al. 1990). Recent observations demonstrated that puffins sometimes forage much farther away, especially overnight, but the large GPS units used in that study might have disrupted foraging patterns (Harris & Wanless 2012).

In summary, puffin dive behavior in our study was similar to that reported elsewhere. Most dives were V-shaped, shallow and diurnal, likely representing individuals foraging on sand eel schools in mid-water near the surface and relatively near the colony (usually <10 km). As extreme multi-prey loaders, puffins were able to exploit abundant prey (small sand eels) that were easily captured (perhaps 1 prey per dive) and therefore did not need to dive deep or fly far to obtain sufficient food. Typically, puffin dives were likely not limited by their oxygen stores or by visibility. By focusing on schools near the surface, it is possible that puffins may use local enhancement (feeding flocks) to cue in on suitable prey.

Comparison between sympatric razorbills and puffins

Reproductive success in 2013 for both of the species was typical. Razorbills *Alca torda* averaged 0.38 chicks per occupied nest compared to the last 10 yr average of 0.39 ± 0.14 , and puffins averaged 0.78 chicks per occupied nest compared to the last 10 yr average of 0.75 ± 0.08 (Büchle et al. 2013). Breeding puffins and razorbills fed on similar prey at our study site in 2013 to those reported by Büchle et al. (2013): they both almost exclusively brought sand

eels to their young during the chick-rearing period, although puffins tended to feed their young smaller sand eels and occasionally sprat (D. Boyle & A. Shoji pers. obs.). There are multiple species of sand eels, differing primarily in size (Harris & Wanless 2012), and it is possible that multiple species of sand eels were involved in the diets of auks in 2013.

Like puffins, razorbill dive data at Skomer were quite similar to dive behaviour recorded elsewhere: in Iceland, where 70% of dives were shallower than 15 m, with most dives between 5 and 10 m deep (Dal'Antonia et al. 2001); the Baltic Sea, where 50% of dives were shallower than 15 m, with most dives between 5 and 10 m deep (Benvenuti et al. 2001); the Gannet Islands, Canada, where average dive depth was ~10 m and duration was ~50 s (Paredes et al. 2008); and the Isle of May, Scotland, where average dive depth was 6.5 m and duration was 23.1 s (Thaxter et al. 2010). Interestingly, the dive depth of razorbills was shallower than puffins, although razorbills are larger; in general, dive depth and duration increases with body mass in auks (Watanuki & Burger 1999). Furthermore, whereas surface intervals in puffins were an accelerating function of dive depth, suggesting progressive constraint associated with on-board oxygen stores, surface intervals in razorbills increased linearly with dive depth, suggesting little constraint. Thus, we suggest that the shallow dive behaviour of razorbills was largely unconstrained by oxygen stores. Indeed, the oxygen stores of puffins (24 ml; Hansen 2003) and razorbills (35 ml; Hansen 2003) would be depleted after 92 and 97 s, respectively, assuming that average dive costs in watts are predicted by the equation: $0.0275(\text{mass in g})^{0.873}$ ('wing-propelled diver' regression by Elliott et al. 2013). Thus, no razorbill dives and <5% of puffin dives would exceed the 'calculated aerobic dive limit' or 'lactate threshold' (Butler 2006), which contrasts substantially with the situation in larger auks that regularly exceed those thresholds (Croll et al. 1992, Elliott et al. 2008). In reality, dive costs are higher for shallow-diving auks than for penguins, especially during buoyant shallow dives, and the 'calculated aerobic limit' may be somewhat overestimated by those simplistic calculations (Elliott et al. 2013).

There are several advantages to the shallow-diving behaviour of razorbills and puffins. Although buoyancy changes substantially in the top 10 m (Watanuki et al. 2003, Lovvorn et al. 2004), meaning that these species spend a substantial proportion of each dive overcoming their buoyancy to descend, they can also use buoyancy to power ascent and

rapidly attack schooling fish from below (Burger et al. 1993). Capturing shallow prey also means that it is relatively easy to track the movement of fish schools from the surface, either because the school is visible from the surface or because large concentrations of surface-feeding predators indicate the school ('local enhancement'; Porter & Sealy 1982, Davoren et al. 2003, Elliott et al. 2009a). Finally, oxygen stores are unlikely to be substantially reduced during short dives, necessitating less time at the surface and therefore a higher proportion of bottom time throughout a dive bout (Croll et al. 1992, Elliott et al. 2008). Apparently, there are many advantages to shallow-diving in auks, as with the exception of guillemots (Croll et al. 1992, Mehlum et al. 2001, Falk et al. 2002, Paredes et al. 2008, Thaxter et al. 2010), few auks regularly dive beyond 15 m in depth despite having the capability to do so (Burger & Powell 1990, Burger et al. 1993, Kuroki et al. 2003, Paredes et al. 2008, Elliott et al. 2010b, Thaxter et al. 2010, Brown et al. 2012).

In many ways, the foraging behaviour of razorbills and puffins was remarkably similar given their differences in size. Certainly, there was no evidence for the clear segregation in dive behaviour and/or flight time apparent in many other seabird assemblages (Table 1). Although puffins dived ~3.5 m deeper, both species used almost exclusively V-shaped dives, implying that, unlike bottom-feeding European shags (Watanuki et al. 2008), neither was obtaining sand eels from the ocean floor; V-shaped dives are primarily associated with capturing prey in mid-water, at least in guillemots (Elliott et al. 2008). In contrast, guillemots have many fewer V-shaped dives than razorbills and puffins, and they forage substantially on benthic fish (Paredes et al. 2008). Both puffins and razorbills bring back multiple, small items to their young, but puffins tended to bring more, smaller items than razorbills, and the longer dives by puffins may have resulted from capturing multiple prey per dive. Thus, it could be expected that puffins have a longer bottom time at a fixed depth as they capture multiple prey items within a school. However, the similarity in shape—as demonstrated by a high proportion of V-shaped dives for both species and the similar relationship between depth and duration—suggests

that there is little bottom time at fixed depth for either species. Our sample size is relatively small, and our study was conducted only within 1 season. Segregation in behaviour amongst species could perhaps occur in years of low but not high prey availability. Thus, future studies could benefit from evaluating behaviour over a longer period. Also, as we were unable to sex individuals within our study, and sex is known to play a strong role in determining dive behavior in auks (Paredes et al. 2005, 2008, Thaxter et al. 2009, Elliott et al. 2010a, Stauss et al. 2012), it is possible that some variation was missed due to unbalanced or missing data from one sex for either species. Similarly, the constraints of accessibility and disturbance to colonies can be severe, and therefore, we were unable to pick individuals randomly. Instead, study birds were chosen at locations with a history of successful breeding and no obvious anomalies. As breeding locations are known to affect foraging behaviour (Soanes et al. 2014), the potential role of sub-colony variation may have been missed.

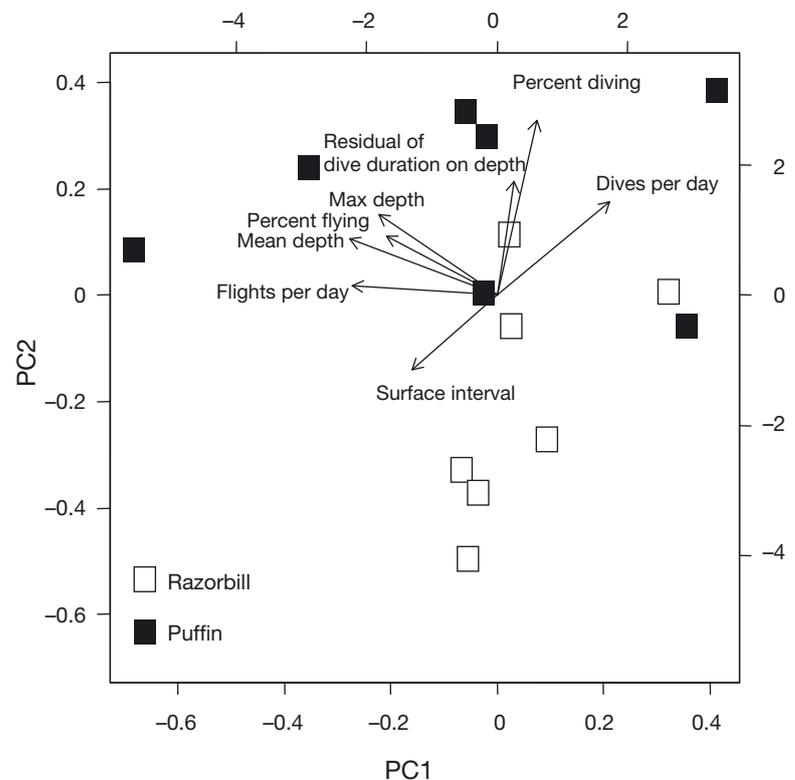


Fig. 2. Principal component analysis of foraging behaviour averaged across each individual. Loadings of different parameters are shown as vectors within the principal component space. Parameters included were the average surface interval duration, average (mean) dive depth, maximum dive depth, average percentage of day spent flying, average percentage of day spent diving, average number of dives per day, average residual of dive duration on depth and average number of flights per day

One potential explanation for the similarity in diving behaviour is that since the diet is similar between the 2 species, they may have used similar conspecific or inter-specific cues to locate food and may have foraged on the same fish shoals. Unlike deep-diving seabirds, puffins feed at low densities on small, low-density shoals of fish near the surface, sometimes associated with tidal rips (Piatt 1990, Wanless et al. 1990, Harris & Wanless 2012). We suggest that razorbills and puffins may have used similar oceanographic cues to feed on similar shoals near Skomer. Another possibility, as shown in guillemots, is that foraging niche may be differentiated only during years of poor food availability (Barger & Kitaysky 2012). When considered together in a multivariate framework, it was clear that many of the parameters were intercorrelated such that the main difference appeared to be that puffins worked harder than razorbills: they dived deeper and spent more time flying and diving (Fig. 2). Puffins' ability to work harder, possibly associated with a 25% lower wing-loading and therefore lower flight costs leaving more residual energy to be expended on diving or additional flying, may lead to higher feeding rates and explain how they can provision their offspring on land for almost twice as long as razorbills.

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Appendix.

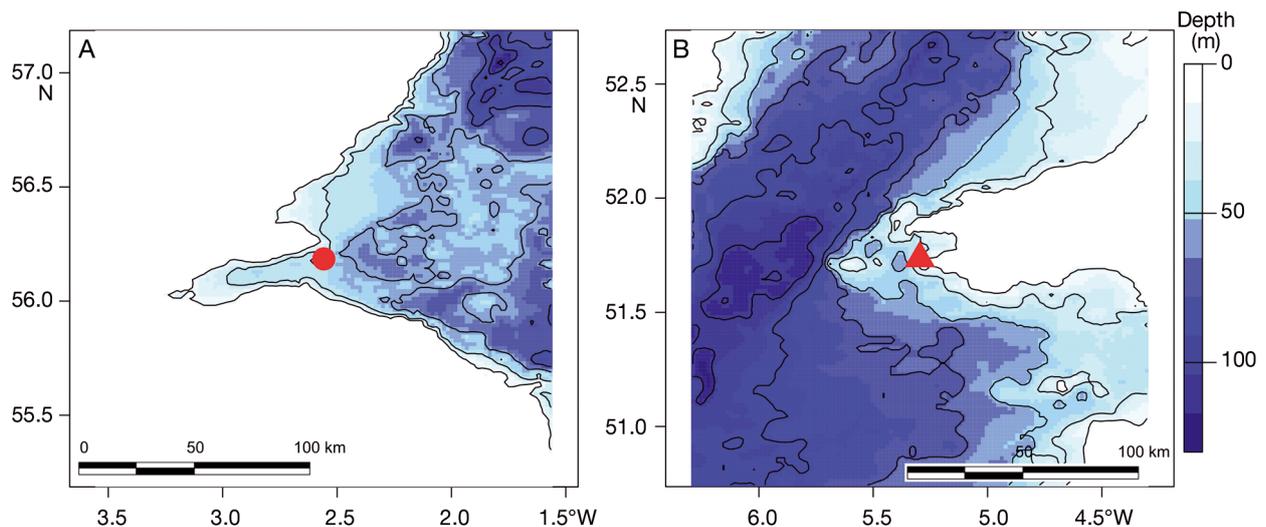


Fig. A1. Bathymetry maps of puffin colony locations at (A) Isle of May and (B) Skomer Island. Red circle indicates the colony at Isle of May, and red triangle indicates the colony at Skomer Island. Scale shown is in meters. Average foraging radius is ca. 8 km and maximum foraging typically 25 km for puffins