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Article

Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season

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Information on seabird foraging behaviour outside the breeding season is currently limited. This knowledge gap is critical as this period is energetically demanding due to post-fledging parental care, feather moult and changing environmental conditions. Based on species' body size, post-fledging parental strategy and primary moult schedule we tested predictions for key aspects of foraging behaviour (maximum dive depth (MDD), daily time submerged (DTS) and diurnal dive activity (DDA)) using dive depth data collected from three seabird species (common guillemot *Uria aalge*, razorbill *Alca torda* and Atlantic puffin *Fratercula arctica*) from the end of the breeding season (July) to mid-winter (January). We found partial support for predictions associated with body size; guillemots had greater MDD than razorbills but MDD did not differ between razorbills and puffins, despite the former being 35% heavier. In accordance with sexual monomorphism in all three species, MDD did not differ overall between the sexes. However, in guillemots and razorbills there were sex-specific differences, such that male guillemots made deeper dives than females, and males of both species had higher DTS. In contrast, there were no marked sex differences in dive behaviour of puffins in July and August in accordance with their lack of post-fledging parental care and variable moult schedule. We found support for the prediction that diving effort would be greater in mid-winter compared to the period after the breeding season. Despite reduced daylight in mid-winter, this increase in DTS occurred predominantly during the day and only guillemots appeared to dive nocturnally to any great extent. In comparison to diving behaviour of these species recorded during the breeding season, MDD was shallower and DTS was greater during the non-breeding period. Such differences in diving behaviour during the post-breeding period are relevant when identifying potential energetic bottlenecks, known to be key drivers of seabird population dynamics.

Keywords: *Alca torda*, energetic bottleneck, *Fratercula arctica*, seabird, *Uria aalge*, winter ecology



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Introduction

Intrinsic factors such as age, sex, reproductive status and body size are known to constrain foraging behaviour across a wide range of taxa and hence play a key role in shaping time activity budgets (King 1974). In addition, a range of extrinsic factors, notably weather conditions and food availability, impact behavioural choices (Ellis and Gabrielsen 2002, Humphries et al. 2004). In many cases both intrinsic and extrinsic effects exhibit temporal predictability e.g. in the timing of breeding or moult, changes in day length and likelihood of bad weather (McNamara and Houston 2008). This interplay between intrinsic and extrinsic factors has helped elucidate how birds make decisions about reproduction during this crucial life history phase (Schlaepfer et al. 2002) and has been particularly well studied in long-lived birds (Phillips et al. 2017). However, in general, much less is known about how intrinsic and extrinsic factors influence foraging behaviour outside the breeding season, particularly in highly mobile species such as seabirds.

Most species of seabird are seasonal breeders and typically experience varying extrinsic conditions throughout their annual cycle. During the breeding season, individual seabird foraging strategies vary intrinsically depending on sex (Kato et al. 2000, Bearhop et al. 2006, Welcker et al. 2009), age (Grecian et al. 2018), parental role (Weimerskirch et al. 2000) and social dominance (González-Solís et al. 2000). The effect of sex on foraging strategy is often associated with size dimorphism, as size differences give rise to competitive exclusion and cause sex-specific niche specialization via trophic segregation or spatial partitioning (González-Solís et al. 2000, Phillips et al. 2017). In addition to size-driven sex-specific behavioural responses, monomorphic seabird species are also often subject to sex-role partitioning, particularly within their parental care strategies (Lewis et al. 2002). Sex-role partitioning can lead to behavioural differences in foraging behaviour, time allocation, habitat preference and scheduling of migration (Phillips et al. 2017).

In addition to influencing behaviour among different categories of individuals within species, intrinsic drivers of variation in foraging behaviour are also key parameters with regard to the ecological segregation of different species of seabird. For example, sympatrically breeding species often forage at different depths in the water column and/or access different food resources in line with size-driven diving capacities; larger species tend to make longer, deeper dives and take larger prey items than smaller species (Wilson 1999, Schreer et al. 2001, Mori and Boyd 2004, Halsey et al. 2006). Additional interspecific differences in breeding season foraging ecology have been observed in sympatric species such as macaroni penguins *Eudyptes chrysolophus* and eastern rockhopper penguins *E. chrysocome filholi*, which forage at different trophic levels (Whitehead et al. 2017), and black-footed albatrosses *Phoebastria nigripes* and Laysan albatrosses *P. immutabilis*, which demonstrate interspecific segregation in their foraging habitats (Hyrenbach et al. 2002). Despite these

intrinsically-determined breeding season behavioural differences, in the majority of cases it is not known whether such disparities persist into the post-breeding period when many species moult, migrate and experience seasonal differences in extrinsic environmental conditions.

Three diving species that often breed sympatrically in the north-east Atlantic, before wintering at sea, are the common guillemot (hereafter guillemot) *Uria aalge*, razorbill *Alca torda* and Atlantic puffin (hereafter puffin) *Fratercula arctica*. During the breeding season their diving capabilities scale allometrically: guillemots, the largest of the three species, make the deepest and longest dives, whilst dive depths and durations of razorbills exceed those of puffins which are the lightest species (Gaston and Jones 1998). Further, guillemots have a higher foraging effort than razorbills during the breeding season (Thaxter et al. 2010). In general, it is not known whether these largely size-driven interspecific differences are maintained outside the breeding season, but Linnebjerg et al (2013) found that guillemots from the north-east Atlantic dived deeper than razorbills immediately after and prior to the breeding season. All three species are significantly heavier outside the breeding season compared to when they are breeding, due to the accumulation of fat reserves (Gaston and Jones 1998). This morphological change could potentially impact the species' post-breeding diving capabilities, since changes in both body size and composition influence diving behaviour via their influence on drag and buoyancy (Sato et al. 2003, Halsey et al. 2006). However, while seasonal changes in body condition affect marine mammal diving behaviour (Richard et al. 2014), this aspect has not yet been investigated in seabirds.

Although guillemots, razorbills and puffins are all considered to be sexually monomorphic, sex-specific behavioural differences have been observed during the breeding season. For example, male razorbills have been found to dive deeper than females (Paredes et al. 2008, but see Linnebjerg et al. 2015) and there is evidence for sex-specific differences in the time budgets of guillemots, razorbills and puffins during the breeding season (Creelman and Storey 1991, Thaxter et al. 2009). However, information on sex-specific foraging behaviour outside the breeding period (defined in this study as the departure of chicks from the breeding colony) is much scarcer. Sex-specific differences in foraging behaviour are predicted to be apparent in guillemots and razorbills where the male parent takes the partly grown chick to sea and continues to feed it for several weeks after the breeding season has ended until it completes its development and becomes independent (Gaston and Jones 1998). In these species males would therefore be expected to spend longer diving per day during male-only parental care, and Paredes et al. (2008) and Burke et al. (2015) did indeed find that male guillemots spent more time diving than females. Males may also adjust diving depth, either increasing it to access resources for chick provisioning, or decreasing it to maximise contact with the chick (Camphuysen 2002, Linnebjerg et al. 2015). In contrast, puffin chicks are independent as soon as they leave the

breeding burrow and the parents provide no further parental care (Harris and Wanless 2011). Thus for this species no sex-specific behavioural differences are predicted.

In addition to sex-specific differences associated with post-fledging care, auk diving behaviour could also be influenced by primary feather moult. Moult is an intrinsically costly process requiring time, energy and nutrients (Ellis and Gabrielsen 2002, Bridge 2006), and the annual replacement of flight feathers is essential to ensure efficiency in both flight and thermoregulation (Murphy 1996, Peery et al. 2008). In guillemots and razorbills, wing moult partially overlaps with the period of male-only post-fledging parental care and therefore the effects of these two phenomenon are likely to occur simultaneously (Gaston and Jones 1998). The scheduling of moult in puffins seems much more variable but typically occurs later than in guillemots and razorbills, with peaks in October and March (Harris et al. 2014). Due to the energetic constraints of moult, coupled with flightlessness (Bridge 2006), moulting auks are thought to favour productive, sheltered areas with predictable prey (Peery et al. 2008, Linnebjerg et al. 2018). However, while it is known that auks continue to dive during their primary wing moult, how their diving capabilities are affected is currently equivocal (Elliott and Gaston 2014). Some studies have concluded that there are likely to be small benefits because of reduced drag (Swennen and Duiven 1991, Thompson et al. 1998, Lovvorn 2004, Bridge 2006). In contrast, a study of captive birds concluded that the smaller wing surface area of moulting birds requires more energy for efficient underwater propulsion and hence diving capability is reduced (Bridge 2004).

These interspecific differences in body size, post-fledging parental strategies and moult schedules are superimposed on seasonally changing environmental conditions during the autumn and first half of the winter (Fort et al. 2009, Daunt et al. 2014). Guillemots, razorbills and puffins from the Isle of May are predominantly located within shelf areas in the North Sea and northeast Atlantic during the post-breeding period and throughout the early winter months (Harris et al. 2010, 2013, 2015a, St John Glew et al. 2018). Auk post-parental care and primary moult both occur before the autumnal equinox when days are comparatively long and

the weather in the region is relatively benign. However, from September onwards day length shortens and the weather becomes harsher with periodic storms, some of which can be prolonged. All three species are wing-propelled pursuit divers which utilise visual cues whilst foraging (Martin and Wanless 2015). Therefore, as light availability limits foraging opportunities (Regular et al. 2011), the majority of their diving occurs during daylight hours (Dall'Antonia et al. 2001) and may become constrained (both temporally and in depth) during the post-breeding period. Seabirds are prone to winter wrecks and high mortality rates during this period (Harris and Wanless 1984, 1996, Fort et al. 2009, 2013, McFarlane Tranquilla et al. 2010), as well as increased energetic requirements (Elliott and Gaston 2014, Burke and Montevecchi 2018). Throughout these seasonal changes in extrinsic conditions, auks must forage sufficiently to acquire enough energy to successfully thermoregulate whilst also building up fat reserves (Fort et al. 2013, Fayet et al. 2016, Anker-Nilssen et al. 2018).

Together, these intrinsic and extrinsic effects form a convenient framework for testing predictions about responses in diving behaviour associated with both intrinsic and extrinsic factors. Comparing these predictions with empirical data allows new insights into the drivers of diving behaviour outside the breeding season. We used this approach to investigate the diving behaviour of guillemots, razorbills and puffins breeding on the Isle of May, a major seabird colony in the north-western North Sea. Long-term studies at this colony have provided population level information on morphometrics, dive behaviour during the breeding season, and the breeding and moulting phenology of these species (Table 1). However, information on the diving behaviour of these populations outside the breeding season is almost totally lacking. We used archival time depth recorders (TDRs) to derive indices of dive performance/activity for each species for each month between the end of the breeding season (July) and mid-winter (January): 1) maximum dive depth (MDD), the maximum depth attained on a dive, 2) daily time submerged (DTS), summed dive durations over a 24 h period, and 3) diurnal dive activity (DDA), the proportion of individuals diving during each hour of the day. Specific

Table 1. Morphological and behavioural characteristics of common guillemot, razorbill and Atlantic puffin populations on the Isle of May (other than puffin winter mass which was obtained from puffins killed in Faroese waters which is where some Isle of May puffins winter). Breeding mass obtained from the literature because mass was not taken from most study individuals to minimise disturbance.

Species	Guillemot	Razorbill	Puffin
Breeding mass (g)	907 ± 55 SD ¹	600 ± 87 SD ¹	380.0 ± 0.71 SE ²
Winter mass (g)	1107 ± 11 SD ³	No data	497.7 ± 7.11 SE ²
Sexual dimorphism	No	No	No
Post-fledging parental care	Yes	Yes	No
Post-fledging care parent	Male	Male	–
Timing of post-fledging parental care	July–August ⁴	July–August ⁴	–
Flightless moult	Yes	Yes	Yes
Timing of flightless moult	July–September ^{5,6}	July–September ⁶	More variable schedule with peaks in October and March ⁷

¹ Thaxter et al. (2010). ² Anker-Nilssen et al. (2018). ³ Harris et al. (2000). ⁴ Gaston and Jones (1998). ⁵ Birkhead (1977). ⁶ Harris and Wanless (1990). ⁷ Harris et al. (2014).

predictions for these dive behaviour indices in response to intrinsic factors (body mass, sex-specific parental care strategies and moult schedule) and extrinsic drivers (seasonal environmental change) are summarised in Table 2.

Material and methods

Data loggers

All fieldwork took place on the Isle of May National Nature Reserve, Scotland (56°11'N, 02°33'W). During the 2005 breeding season, 30 adult guillemots brooding chicks were captured at the breeding site using a 7 m noose pole and fitted with TDRs (LT2400, Lotek Wireless, St John's, Newfoundland, Canada, 36×11 mm) attached to Darvic leg-rings. During the 2008 breeding season, breeding razorbills (n=24) were captured in the same way as guillemots and breeding puffins (n=30) were caught in their burrows. For both species TDRs (G5, CEFAS, Lowestoft, UK, 31×8 mm) were again attached using Darvic leg-rings. In all cases the attachment process took < 5 min. The mass of the TDR plus rings were 6.5, 3.3 and 3.0 g, 0.7, 0.6 and 0.8% of the breeding body mass of the respective species (Table 1). Three to five body feathers were collected from retrieved birds

under UK Home Office Licence, to enable birds to be sexed using two CHD I genes (Griffiths et al. 1996). Birds were recaptured during the breeding season following deployment, i.e. 2006 for guillemots and 2009 for razorbills and puffins. The same methods as for deployment were utilised in order to recapture birds and the TDRs were removed. Retrieval rates were 43.3, 54.2 and 40.0% for guillemots, razorbills and puffins, respectively.

Our original aim was to collect data over the entire non-breeding period (July–April for our study populations). However, this was only possible for guillemots for which all the TDRs were still recording data when they were retrieved. In the case of razorbills and puffins some TDRs failed completely while others failed progressively during the autumn so that the number of individuals contributing data declined over time. We were thus only able to compare dive behaviour of the three species for the period July–January. Details of the sampling periods and number of days of data are provided in Supplementary material Appendix 1.

To record data over an extended period, TDRs were set to take a depth reading every 1) 16 s for a 24 h period every 30 d (guillemots, n=9 retrieved birds), 2) 32 s for a 24 h period every 15 d (guillemots, n=4), 3) 3 s for a 24 h period every 10 d (razorbills, n=7; puffins, n=6) or 4) 30 s for a 24 h period every day (razorbills, n=6; puffins, n=6). Two sampling rates

Table 2. Predictions of hypotheses on the causes of differences in diving behaviour outside the breeding season in common guillemots, razorbills and Atlantic puffins from the Isle of May.

Hypothesis	Predictions		
	Maximum dive depth (MDD)	Daily time submerged (DTS)	Diurnal diving activity (DDA)
Interspecific and sex-specific body mass	Guillemot > razorbill > puffin; no sex-specific differences.	Higher foraging effort of guillemots than razorbills in breeding season to persist into non-breeding season. No specific predictions for puffins, or for sex differences.	No interspecific or sex differences.
Post-fledging parental care	Sex-specific differences in guillemots and razorbills in July/August, but not puffins. Alternative predictions: a) males may reduce dive depth to maximise contact with surface-bound chick; b) males may increase dive depth to access particular prey for provisioning.	Males > females in guillemots and razorbills, due to the costs of provisioning offspring. No specific predictions for puffins.	No interspecific or sex differences.
Primary wing moult	Change in guillemots and razorbills in August/September associated with dive efficiency and energetic costs during moult; direction not clear because of equivocal evidence of dive efficiency at this time; no direct sex-specific differences expected as a result of moult. No specific prediction for puffins where timing of moult is more variable and unknown in these individuals.	As MDD.	No interspecific or sex differences.
Seasonal environmental change	Progressive change in dive depth with changing body composition and declining light levels.	Progressive increase between July and January as food availability changes and energetic costs increase.	Alternative predictions: a) greater use of night-time hours as season progresses in response to shortening day length and altered conditions; b) increasingly constrained to the middle of the day as daylight decreases.

were used for each species to balance resolution with number of days of data, due to the limited memory size of the TDRs. The memory size of the TDRs used on the guillemots was smaller, necessitating a 16/32 s protocol compared to the 3/30 s protocol used on razorbills and puffins.

Fledging dates were not known for any of the TDR birds. However, mean fledging dates for all three species were available from monitoring plots. We therefore used these population-level values to define the start of the non-breeding period as 10 July 2005 for guillemots, 30 June 2008 for razorbills and 18 July 2008 for puffins. Data collected prior to this were assumed to come from breeding birds (Supplementary material Appendix 2).

Data processing

A purpose-written script for IGOR Pro (Wavemetrics Inc., Portland, OR, USA, 2000, ver. 6.37) was used to determine values of dive depth and duration from all the TDR-recorded depth data from the 24 h sampling periods. After visually correcting for device drift (Elliott and Gaston 2009), the dataset was filtered to remove values of < 1 m that were likely to be associated with non-diving activities such as washing (Shoji et al. 2016). Maximum dive depth (MDD) was extracted for each derived dive. Thaxter et al. (2009) found strong bimodality in the dive depths of guillemots from the Isle of May during the breeding season. However, we found no evidence of bimodality outside the breeding season for any of the species and thus did not classify dives as shallow or deep (Supplementary material Appendix 3). In addition to MDD, dive duration was also extracted for each dive and was summed to calculate a metric of daily time submerged (DTS). The loggers with lower sampling rates (30 and 32 s) will have missed some shorter dives, which could have resulted in an underestimate of DTS and/or an overestimate of MDD. However we expected the lack of short dives to be counteracted by an overestimation of dive duration, resulting in no overall effect of DTS. We investigated this potential issue in two ways. First, we compared the empirical estimates of MDD and DTS using the two sampling rates for each species and found that they did not differ significantly (Supplementary material Appendix 4). Second, we conducted a simulation exercise where we compared DTS at sampling intervals of 1, 2, 4, 8, 16 and 32 s and found that it was consistent across sampling frequencies (Supplementary material Appendix 4). We therefore concluded that these measures were robust to variation in sampling rate and so we excluded sampling rate from analyses. Because of this sampling issue, from hereon we refer to 'dive indices' as opposed to 'dives'.

To determine changes in patterns of daily dive activity (DDA) for each species during the non-breeding period, the proportion of individuals recorded diving during each hour of the day was extracted for each month. An individual that showed evidence of one or more dives in a given hour in a given month was classified as having undertaken diving activity.

Statistical analyses

All analyses were computed within the R statistical Framework (R Core Team). Mixed models, performed using the 'lmer' function in the 'lme4' package (Bates et al. 2015), were used to evaluate species and sex-specific differences in MDD and DTS. Maximum dive depth data were log transformed to help approach normality prior to analyses. Initially, a three-way interaction between species, sex and month (where month was an ordered categorical variable in order to allow for non-linear month-by-month responses) was tested for significance. This interaction allowed us to consider both interspecific and sex effects on temporal differences in MDD and DTS. Individual bird ID was included as a random factor to account for potential non-independence. When analysing MDD, day since deployment was also included as a random factor to account for a lack of independence between dives performed on the same day. To interpret the interaction terms, post hoc comparisons were performed using estimated marginal means statements with the 'emmeans' package (Lenth 2019). Based on the available information on the scheduling of post-fledging parental care and primary wing moult in the Isle of May populations, July and August were assumed to be the months when male guillemots and razorbills were predominantly engaged in post-fledging parental care and August and September were assumed to be the months when guillemots and razorbills (both sexes) moulted and regrew their primaries (Table 1). The non-breeding period was further divided into an autumn (July–September) and winter period (October–January) with environmental conditions in the latter assumed to be more severe.

Small sample sizes for razorbills and puffins, particularly from November onwards, precluded using formal analytical approaches such as GAMMs and GLMMs to investigate monthly changes in DDA. Instead, a visual approach was used to compare the proportion of birds recorded diving in each hour of the day. A similar approach has been adopted in studies of diurnal patterns in seabird commuting behaviour (Padgett et al. 2017) and diving behaviour in turtles (Hays et al. 2001). Unless stated otherwise all values are means \pm standard error and all times are GMT.

Data deposition

All data are available from the Environmental Information Data Centre: <<https://doi.org/10.5285/6ab0ee70-96f8-41e6-a3e3-6f4c31fa5372>>) (Dunn et al. 2019).

Results

Diving data

We recorded a total of 21 008 dive indices from guillemots (mean 1616 dive indices per individual, $n = 13$ individuals, range 1043–2551), 111 904 dive indices from razorbills

(mean 8606 dive indices per individual, $n = 13$ individuals, range 2603–20 520) and 49 222 dive indices from puffins (mean 4474 dive indices per individual, $n = 12$ individuals, range 686–11 470). Sample sizes for puffins and razorbills decreased progressively during the study due to TDR failures (see Supplementary material Appendix 1 for details). We note that the number of dives is probably an underestimate for all three species (Supplementary material Appendix 4).

Overall frequencies for MDD and DTS outside the breeding season indicated that in all three species dive depths and daily diving effort were highly variable (Fig. 1). Deepest depths were 118.2, 47.4 and 38.4 m for guillemot, razorbill and puffin respectively while 10.65, 8.15 and 9.47 h per day were the maximum daily times submerged. However, in general, MDDs outside the breeding season were relatively shallow with 59.8, 98.9 and 97.0% dives < 15 m in guillemots, razorbills and puffins respectively while average DTS was 4.86 ± 0.18 , 2.10 ± 0.05 and 4.07 ± 0.12 h for the three species (Fig. 1). The strong bimodality in MDD in guillemots recorded during the preceding breeding season (Supplementary material Appendix 2) was no longer present; MDD in all species was shallower than during the preceding breeding season, despite body mass increasing after the breeding season, but DTS was greater (Supplementary material Appendix 2).

Interspecific body mass effects

Based on interspecific differences in body mass we predicted that MDD outside the breeding season would be greater in guillemots than razorbills, and greater in razorbills than puffins (Table 2). Data from TDRs indicated that mean MDD for guillemots was indeed deeper than for razorbills (mean 17.6 ± 0.1 m c.f. 4.2 ± 0.1 m). However, mean MDD of razorbills was slightly shallower than that of puffins (4.2 ± 0.1 m c.f. 5.0 ± 0.1 m) (Table 3, Fig. 1).

We found support for our prediction that the higher foraging effort of guillemots than razorbills in the breeding season would persist into the non-breeding season. Thus, on average, DTS was higher in guillemots than in razorbills (4.86 ± 0.18 h and 2.10 ± 0.05 h respectively; Table 3). Mean DTS for puffins was similar to that of guillemots (4.07 ± 0.12 h; Fig. 2).

In accordance with our predictions that overall MDD and DTS would not differ between the sexes because all three species are sexually monomorphic, we found no evidence of a main effect of sex for any of the species (Table 3).

Post-fledging parental care

Sex-specific differences in guillemot and razorbill dive behaviour in July and August are predicted as a result of males providing post-fledging parental care of chicks during these

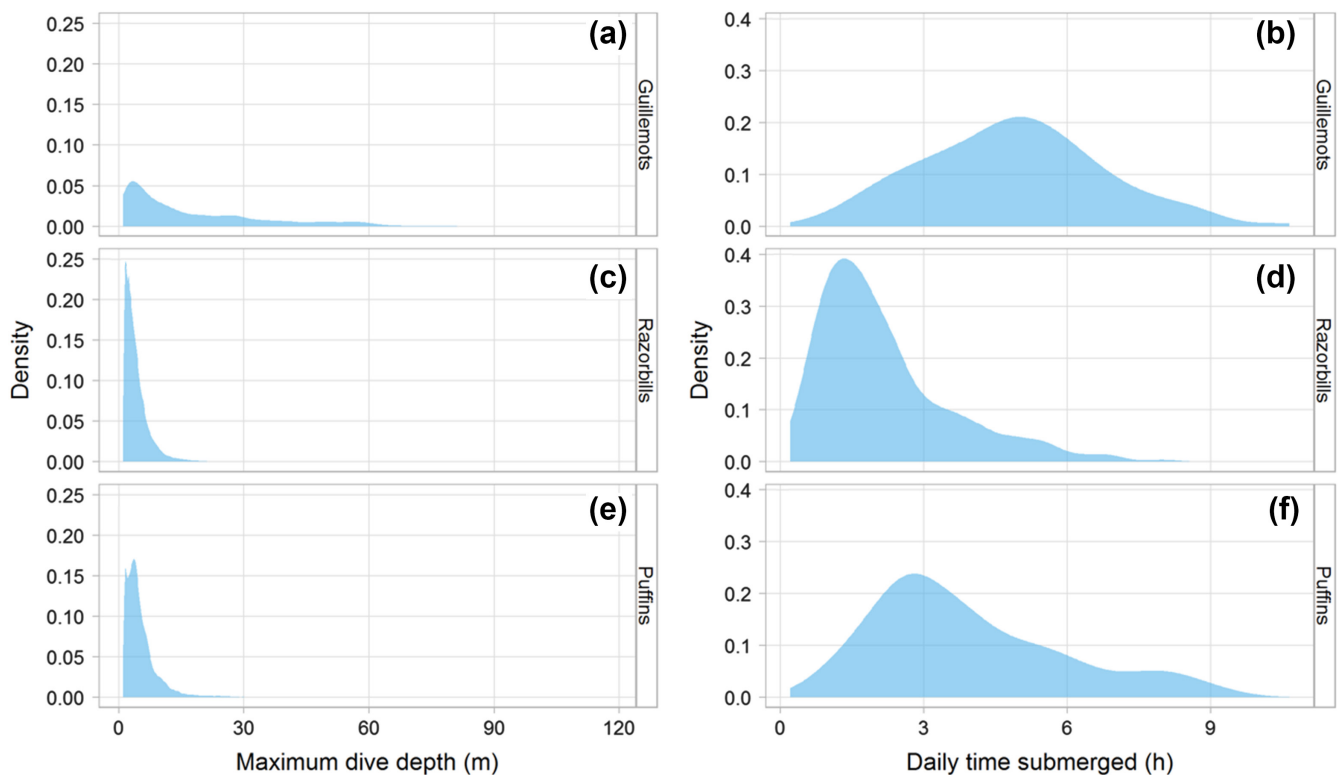


Figure 1. Density plots displaying the distribution of maximum dive depths (MDD; plots a, c and e) and daily time submerged (DTS, plots b, d and f) of common guillemots, razorbills and Atlantic puffins between July and January.

Table 3. Model outputs from linear mixed models investigating the factors influencing maximum dive depth (MDD) and daily time submerged (DTS) of common guillemots, razorbills and Atlantic puffins from the Isle of May during the non-breeding period (July–January).

Model term	df	MDD		DTS	
		χ^2	p	χ^2	p
Species	2	77.61	<0.01	117.07	<0.01
Month	6	1375.29	<0.01	85.17	<0.01
Sex	1	0.50	0.48	2.09	0.15
Species × Month	11	2518.88	<0.01	151.82	<0.01
Species × Sex	2	3.71	0.16	4.09	0.13
Month × Sex	6	514.13	<0.01	127.03	<0.01
Species × Month × Sex	9	2964.46	<0.01	27.13	<0.01

months. For MDD the predicted direction of the difference is unclear, since increased MDD would allow males to exploit a greater part of the water column while decreased MDD would minimise risks of males getting separated from their chicks. The TDR data indicated a significant sex × month interaction (Table 3) and post hoc tests indicated that MDD was markedly deeper in male guillemots compared to females in July (mean 55.9 ± 1.4 m and 16.5 ± 0.6 m respectively) and August (mean 18.4 ± 0.5 m and 9.2 ± 0.2 m respectively), but there was no evidence of significant sex-related depth partitioning in razorbills (Fig. 2). DTS values are predicted to be greater in males than females because of additional effort required to provision the chick until it becomes independent. In accordance with this, DTS of male guillemots

in July was more than double that of females (10.65 h and 2.01 h respectively, although $n=1$), but no difference was apparent in August (4.42 ± 0.57 h and 4.09 ± 0.54 h for males and females respectively), while in razorbills, DTS of males was longer in July (2.85 ± 0.22 h and 2.14 ± 0.13 h for males and females respectively) and markedly longer than females in August (2.98 ± 0.32 h and 1.20 ± 0.52 h for males and females respectively; Fig. 3). Puffins do not provide sex-specific, post-fledging parental care and we found no evidence of marked sex differences in either MDD or DTS in July (4.01 ± 0.36 h and 3.09 ± 0.21 h for males and females respectively) or August (2.99 ± 0.21 h and 2.76 ± 0.12 h for males and females respectively).

Primary wing moult

The timing of primary moult in guillemots and razorbills overlaps with the period of post-fledging parental care but also extends into September. Unlike post-fledging parental care, no sex differences in dive behaviour are expected as a direct consequence of moult. However, inter-specific differences in MDD and DTS may arise from differences in diving efficiency and the energetic costs of moult. The direction of predicted differences are equivocal due to uncertainty in whether the loss of primaries increases or reduces diving efficiency (Table 2). As reported above, MDD did differ between male and female guillemots in July and August, suggesting that post-parental care effects were more important in this species. In contrast, no marked sex effects were apparent

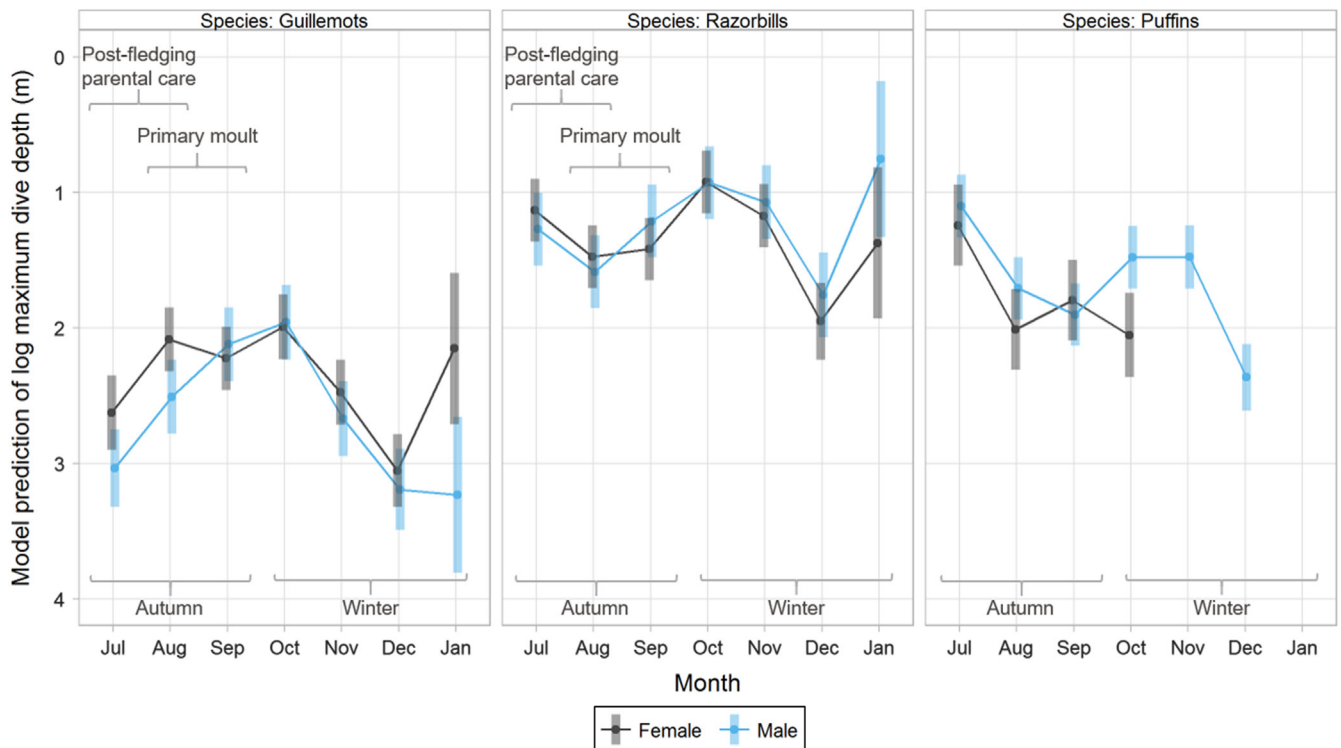


Figure 2. Estimated marginal means and 95% confidence intervals of log maximum dive depth (MDD) under the effect of the interaction of species, sex and month outside the breeding season. The y-axis has been inverted and 0 therefore equates to the water surface.

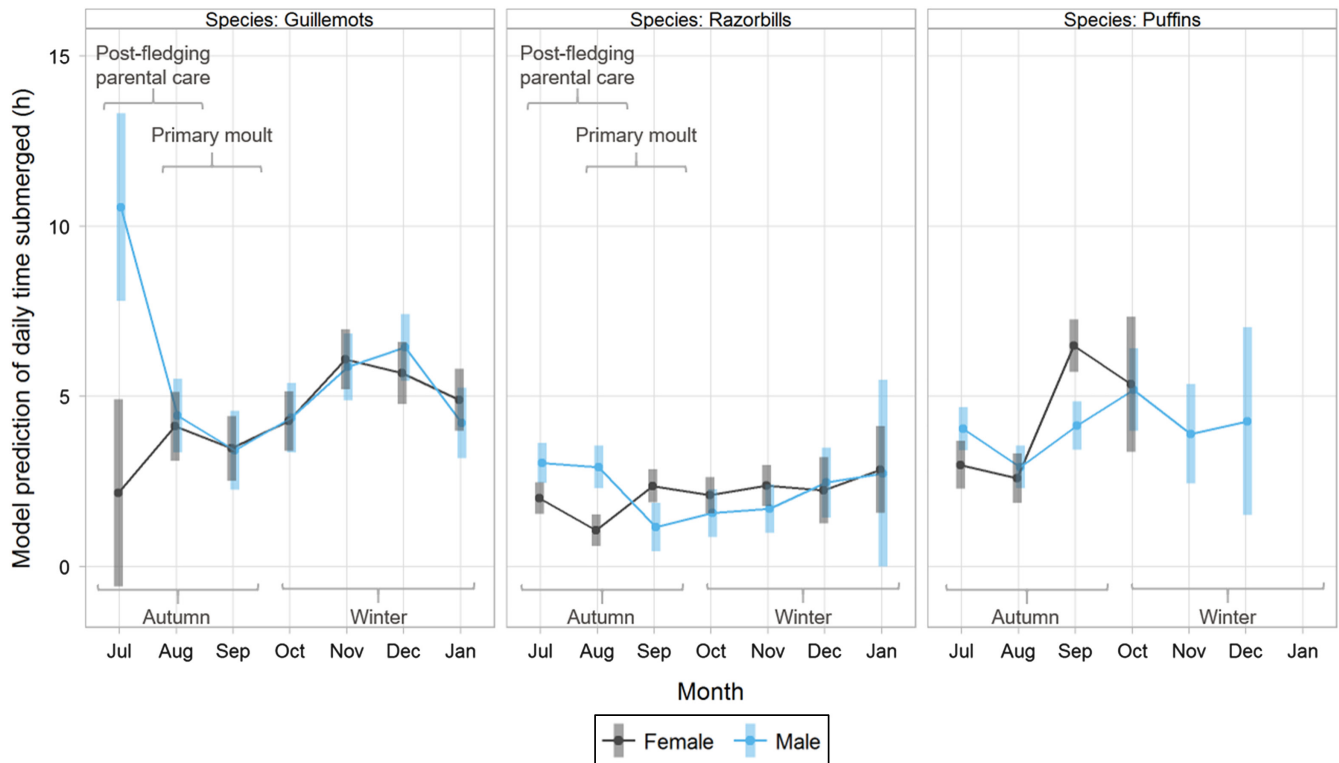


Figure 3. Estimated marginal means and 95% confidence intervals of daily time submerged (DTS) under the effect of the interaction of species, sex and month outside the breeding season.

in razorbills. In both species, MDD in August and September was shallow relative to later in the season (Fig. 2), indicating that in general, birds were not making deep dives while they were moulting. However, MDD was lowest in October when most guillemots and razorbills should have completed their moult. Timing of primary moult in puffins is more variable than in guillemots or razorbills and was unknown in study individuals but was most likely to have occurred in October. There was no evidence that puffin MDD in October was markedly different to other months (Fig. 2). Values for DTS in October were relatively high but sample sizes were small making comparisons difficult.

Seasonal environmental change

Predictions associated with changes in environmental conditions between the end of the breeding season and mid-winter are for MDD to change, DTS to increase and DDA to show changes (either more constrained use, or greater use of night-time hours). These changes are predicted because day length shortens, light levels at depth are reduced due to the lower angle of the sun, and conditions change as a result of worsening weather within the North Sea and northeast Atlantic. We found that values of MDD for all three species increased rather than decreased between October and December, although values for puffin in November and December were based on a single bird (Fig. 2, Table 3). Our prediction for DTS was partially supported since DTS was higher for

guillemots in November and December (Fig. 3). DTS in razorbills increased slightly between October and December. No clear trend was apparent in puffins (Fig. 3), but sample sizes were too small to allow reliable comparisons.

There were seasonal changes in DDA (Fig. 4), such that there was a gradual delay in the start time of diving and an advancement in the end time in razorbills and puffins as day length shortened. In contrast, guillemots dived across the 24-h period throughout the winter, with 28% of diving occurring outside the hours of 08:00–20:00 (Fig. 4).

Discussion

Identifying the drivers of behaviour outside the breeding season and understanding their implications for energy budgets and energetic bottlenecks have recently been highlighted as research priorities (Cherel et al. 2016). Our study provides the first comprehensive assessment of the factors influencing key aspects of overwinter diving behaviour in three species of auk that together make up a major component of the seabird community wintering in the North Atlantic (Grandgeorge et al. 2008). We found that both intrinsic and extrinsic factors drive the diving behaviour of these species in ways which differ from those operating during the breeding season.

Overall, MDDs of all three species were well within their physiological capacities as indicated by maximum

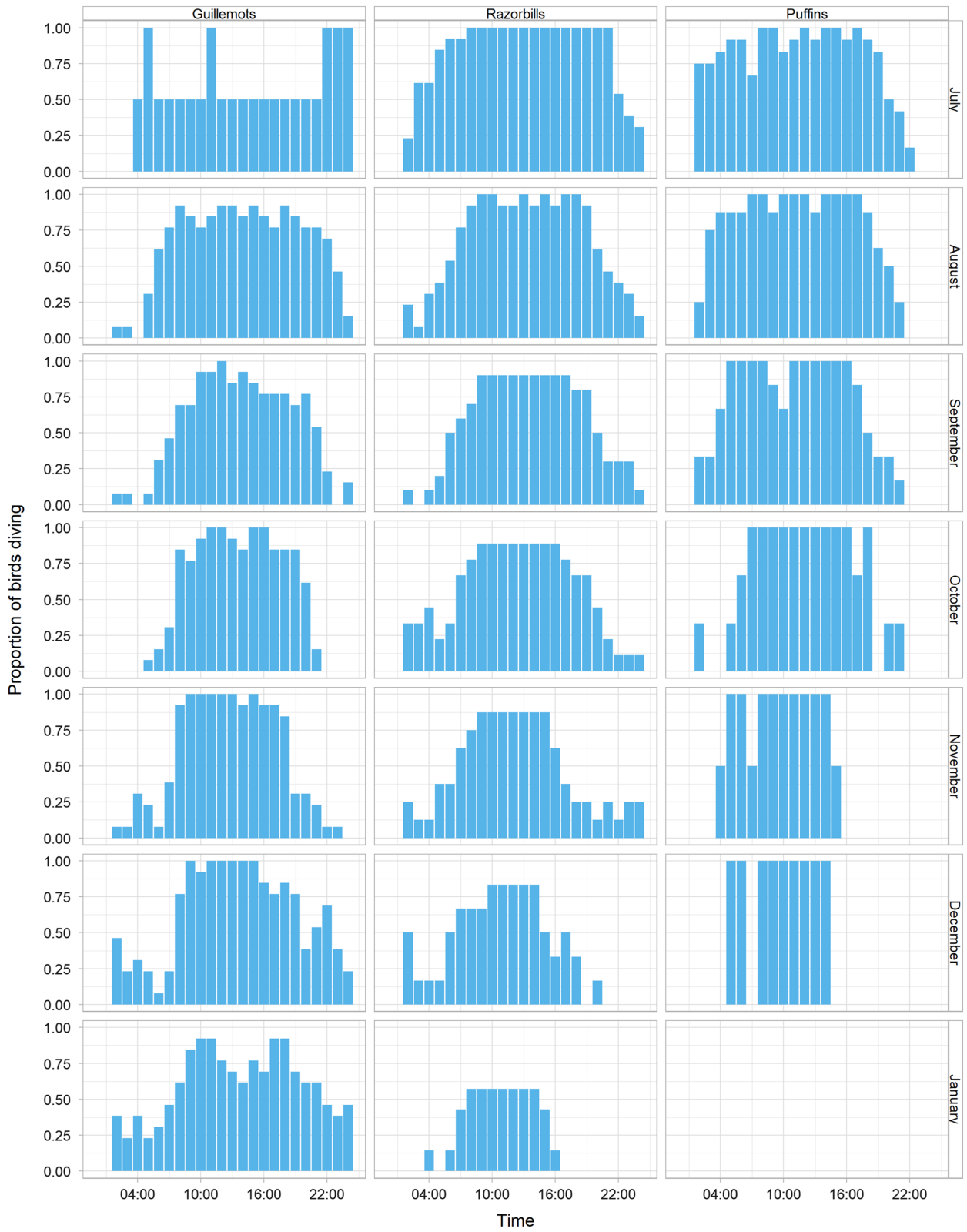


Figure 4. Changes in diurnal diving activity (DDA) of common guillemots, razorbills and Atlantic puffins from July to January.

recorded dive depths of 138, 140 and 68 m for guillemot, razorbill and puffin respectively (Burger and Simpson 1986, Jury 1986). However, studies elsewhere have recorded auks diving deeply outside the breeding season. For example, guillemots and razorbills from colonies in southwest Greenland had mean dive depths of 27.4 m and 8.6 m in September (Linnebjerg et al. 2013), compared to mean maximum depths of 10.9 m and 4.7 m for these species during the same month in our study. Guillemots, razorbills and puffins all show increases in body mass after the breeding season (Harris et al. 2000, Anker-Nilssen et al. 2018), presumably due to deposition of fat reserves. Increased fat deposits are likely to increase the diving costs required to overcome buoyancy (Lovvorn 2004, Watanuki et al. 2006), especially given the shallow depths observed here. Thus the progressive increase in MDD outside the breeding season may suggest that increased buoyancy is driving deeper dives, but the general lack of deep diving indicates that diving behaviour of auks during the post-breeding period is predominantly driven by extrinsic factors such as light levels and prey distribution as opposed to physiological constraints. Despite the wintering areas of guillemots, razorbills and puffins from the Isle of May having typical water depths of < 100 m, and in many cases < 50 m, there was no evidence that dive depth was restricted by the bathymetry in these relatively shallow areas, with dives by all species being concentrated mainly within the top 20 m of the water column.

When comparing our empirical data from bird-borne TDRs with predictions from different dive behaviour hypotheses, we found partial support for responses in accordance with interspecific differences in body mass and associated mass-specific oxygen stores (Watanuki et al. 2006, Paredes et al. 2008, Thaxter et al. 2010). Thus outside the breeding season, MDD of guillemots was markedly deeper than that of razorbills (Table 3, Fig. 1). However, despite razorbills being 35% heavier than puffins, there was no significant difference in MDD between these two species with both making predominantly shallow dives (means of 4.2 ± 0.1 m and 5.0 ± 0.1 m respectively and > 90% of records being < 5 m). Interspecific depth segregation in guillemots and razorbills has previously been recorded during the chick-rearing period on the Isle of May with the former making significantly longer, deeper dives (Thaxter et al. 2010), while on Skomer Island, Wales, Shoji et al. (2015) found that puffins accessed deeper dive depths than razorbills during the breeding season despite their lower body mass.

Interspecific differences in dive depth have been linked to differences in chick provisioning strategies: guillemots are obligate single-prey loaders and thus require larger prey items for the chick than razorbills and puffins which are multiple-prey loaders and have the option of bringing back many smaller prey items (Wilson et al. 2004, Thaxter et al. 2010, Harris and Wanless 2011). Razorbills and puffins may therefore make shallower dives in order to target shoals of smaller sized but more numerous prey items (Ouweland et al. 2004, Thaxter et al. 2010, 2013,

Shoji et al. 2015, Chimienti et al. 2017). Although guillemot MDD decreased after the breeding season, greater depth usage compared to the other two species persisted through to January (Fig. 3). The evidence to date suggests that depth segregation among these species is maintained throughout the winter and that guillemots target different prey. In the case of the Isle of May auk community, these conclusions accord well with stable isotope analyses which indicate that guillemots consistently forage at a higher trophic level than razorbills and puffins during winter moult periods (St John Glew et al. 2018).

In addition to the consistent difference in depth usage among species, razorbills also continued to have significantly lower DTS than guillemots outside the breeding season, matching interspecific differences in foraging effort during the breeding season (Thaxter et al. 2010). However, data from more populations and years are required to establish why guillemots have higher DTS than the other two auk species both during the breeding season and the subsequent non-breeding period.

We also found support for the body mass hypothesis with respect to the overall absence of strong intraspecific sex differences in diving behaviour, consistent with the lack of sexual dimorphism in all three species. However, although sex was not significant as a main effect for either MDD or DTS for any of the species, we did find evidence of intraspecific sex differences in some months. The timing of these sex differences accorded well with predictions based on interspecific differences in post-fledging parental care which occurs predominantly in July and August. Thus in guillemots and razorbills, the two species in which the male parent takes the partially grown chick to sea and provides it with food and protection for at least a month, MDD was deeper in male compared to female guillemots, while DTS was longer in male compared to female guillemots and razorbills (Table 3, Fig. 3). Shallower dives have been suggested as a way of maximising contact between males and their chicks thereby reducing risks of predation and/or the two getting separated in rough sea conditions (Camphuysen 2002). However, we found no support for this, for guillemot MDD was deeper not shallower in males, particularly in July and August, suggesting that they may have dived deeper to access prey required for chick provisioning. Similarly Burke et al. (2015) found that male guillemots from colonies in Newfoundland, Canada made deeper dives whilst providing post-fledging parental care. Elevated DTS, which was recorded in both species, was consistent with the male providing the additional nutritional demands of the growing chick (Paredes et al. 2008, Burke et al. 2015), although the timing of increased effort differed between the species with the sex difference being more marked for guillemots in July and for razorbills in August. Differences in sex-specific foraging effort during post-fledging parental care have previously been shown in both common and Brünnich's guillemots *Uria lomvia*, with male birds again spending more time diving at this time (Elliott and Gaston 2014, Burke et al. 2015). An increase

in DTS during the post-fledging period has not previously been demonstrated in razorbills. Clearly there is a need for more information on individual-level behaviour during this crucial period in this species. In puffins, where neither sex provides post-fledging parental care, the data matched our predictions such that there were no marked sex differences in either MDD or DTS in July or August.

In guillemots and razorbills, the main moult, including the replacement of flight feathers when birds are flightless, is concurrent with the July/August post-fledging parental care period but also extends into September. In the Isle of May populations wing moult appears to be complete by early October because guillemots start attending the colony again in mid to late October (Harris and Wanless 2016). Dive behaviour during August and September indicated that in guillemots MDD was lower than later in the season and DTS was also relatively low. Such patterns are consistent with guillemots having successfully located, and remained in, productive waters with abundant prey (Peery et al. 2008, Linnebjerg et al. 2018). In contrast, effects in razorbills were much less pronounced with no clear changes associated with the moult period, further highlighting the need for more data on dive behaviour outside the breeding season for this species. Timing of moult in puffins appears to be much more variable than guillemots and razorbills. The available evidence suggests that puffins from the Isle of May population are most likely to moult in October or March (Harris et al. 2014). The timing of moult was unknown in our study individuals, but as with razorbills, there was little evidence that moult had any marked effect on dive behaviour in terms of MDD or DTS.

Coinciding with seasonal changes in environmental conditions, we observed an increase in DTS within both guillemots and razorbills between October and January compared to between July and September (Fig. 3). Guillemots and razorbills were also found to increase MDD (Fig. 2), in keeping with our prediction that dive depth would increase with seasonal changes in body mass, and in accordance with other studies of guillemot winter diving behaviour (Fort et al. 2013, Elliott and Gaston 2014, Burke and Montevecchi 2018). Deeper dives would allow birds to avoid the increased wave action and associated turbulence near the surface during storms (Finney et al. 1999). In addition, birds may have had to dive deeper in order to access energy-dense prey which remain at depth during the winter as surface waters cool (Burke and Montevecchi 2018). Increases in DTS may also be due to birds working harder in order to capture potentially scarcer prey, particularly when light levels are lower. However, reasons for differences in DTS are difficult to interpret without independent data on the distribution of prey (Fayet et al. 2016). Further multidimensional studies are therefore needed to disentangle the extrinsic influences on diving behaviour during the post-breeding period.

Progressive failures of TDRs on puffins meant that sample sizes from October onwards were very small, greatly hampering evaluation of dive behaviour during the winter period. Winter is thought to be a period of high mortality in puffins

(Harris et al. 2010, Harris and Wanless 2011) and future studies should therefore seek to address the links between foraging behaviour and survival during this time in this species.

The start of winter also signals an increasing restriction in terms of the temporal availability of daylight. Across all three species there was evidence that time of diving was increasingly constrained by daylight hours as the winter progressed with the start of diving delayed in the morning and the end of diving advanced in the afternoon/evening (Fig. 4). This pattern was most obvious in puffins which apparently did not dive at night, suggesting they may have higher dependence on light to locate prey than the other two species (Martin and Wanless 2015, Shoji et al. 2015). This would accord with puffin diet outside the breeding season which is typically made up of small, often semi-translucent, prey items that are difficult to locate (Hedd et al. 2010, Harris et al. 2015b, Martin and Wanless 2015). In contrast, several studies have recorded guillemots foraging across the 24-h period (Hedd et al. 2009, Regular et al. 2010, 2011). We also found that some Isle of May guillemots continued to dive across the diel cycle, further demonstrating their ability to successfully forage under nocturnal light levels. Razorbill vision is more similar to that of guillemots than puffins (G. R. Martin unpubl.) and razorbills have also previously been found to dive at night, although shallower depths were accessed in the late evenings and early mornings (Dall'Antonia et al. 2001, Linnebjerg et al. 2015). In our study we also recorded evening and early morning diving in razorbills but nocturnal dive behaviour was not as prevalent as in guillemots (Fig. 4).

In conclusion, we found evidence of interspecific, sex-specific and temporal segregation in maximum dive depth and daily time submerged across three auk species outside the breeding season. In combination these results demonstrate how intrinsic and extrinsic effects influence diving behaviour at this time. Such data are central to establishing when key energetic bottlenecks in the annual cycle in both sexes in different species occur. Quantifying when and where these bottlenecks occur will improve predictions of future climate impacts and assessments of the consequences of human activities such as offshore renewable developments on seabird species.

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References

- Anker-Nilssen, T., Jensen, J. K. and Harris, M. P. 2018. Fit is fat: winter body mass of Atlantic puffins *Fratercula arctica*. – *Bird Study* 65: 451–457.
- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. lme4: linear mixed-effects models using Eigen and S4. – *J. Stat. Softw.* 67: 1–48.
- Bearhop, S., Phillips, R. A., McGill, R., Cherel, Y., Dawson, D. A. and Croxall, J. P. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. – *Mar. Ecol. Prog. Ser.* 311: 157–164.
- Birkhead, T. R. 1977. Molt of the guillemot *Uria aalge*. – *Ibis* 119: 80–85.
- Bridge, E. S. 2004. The effects of intense wing molt on diving in alcids and potential influences on the evolution of molt patterns. – *J. Exp. Biol.* 207: 3003–3014.
- Bridge, E. S. 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. – *Mar. Ornithol.* 34: 7–19.
- Burger, A. E. and Simpson, M. 1986. Diving depths of Atlantic puffins and common murres. – *Auk* 103: 828–830.
- Burke, C. M. and Montevecchi, W. A. 2018. Taking the bite out of winter: common murres (*Uria aalge*) push their dive limits to surmount energy constraints. – *Front. Mar. Sci.* 5: 63.
- Burke, C. M., Montevecchi, W. A. and Regular, P. M. 2015. Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. – *PLoS One* 10: e0141190.
- Camphuysen, K. C. J. 2002. Post-fledging dispersal of common guillemots *Uria aalge* guarding chicks in the North Sea: the effect of predator presence and prey availability at sea. – *Ardea* 90: 103–119.
- Cherel, Y., Quillfeldt, P., Delord, K. and Weimerskirch, H. 2016. Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds molt. – *Front. Ecol. Evol.* 4: 3.
- Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M. J. and Scott, B. E. 2017. Taking movement data to new depths: inferring prey availability and patch profitability from seabird foraging behavior. – *Ecol. Evol.* 7: 10252–10265.
- Creelman, E. and Storey, A. E. 1991. Sex differences in reproductive behavior of Atlantic puffins. – *Condor* 93: 390–398.
- Dall'Antonia, L., Gudmundsson, G. A. and Benvenuti, S. 2001. Time allocation and foraging pattern of chick-rearing razorbills in northwest Iceland. – *Condor* 103: 469–480.
- Daunt, F., Reed, T. E., Newell, M., Burthe, S., Phillips, R. A., Lewis, S. and Wanless, S. 2014. Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. – *Ecology* 95: 2077–2083.
- Dunn, R. E., Wanless, S., Green, J. A., Harris, M. P. and Daunt, F. 2019. Data from: Dive times and depths of auks (Atlantic puffin, common guillemot and razorbill) from the Isle of May outside the breeding season. – Environmental Information Data Centre, <<https://doi.org/10.5285/6ab0ee70-96f8-41e6-a3e3-6f4c31fa5372>>.
- Elliott, K. H. and Gaston, A. J. 2009. Accuracy of depth recorders. – *Waterbirds* 32: 183–191.
- Elliott, K. H. and Gaston, A. J. 2014. Dive behaviour and daily energy expenditure in thick-billed murres *Uria lomvia* after leaving the breeding colony. – *Mar. Ornithol.* 42: 183–189.
- Ellis, H. I. and Gabrielsen, G. W. 2002. Energetics of free-ranging seabirds. – In: Whittow, G. C. and Rahn, H. (eds), *Seabird energetics*. Plenum Press, N.Y., pp. 359–408.
- Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M. and Guilford, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. – *Behav. Ecol.* 27: 1061–1072.
- Finney, S. K., Wanless, S. and Harris, M. P. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the common guillemot *Uria aalge*. – *J. Avian Biol.* 30: 23–30.
- Fort, J., Porter, W. P. and Grémillet, D. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. – *J. Exp. Biol.* 212: 2483–2490.
- Fort, J., Steen, H., Strom, H., Tremblay, Y., Gronningsaeter, E., Pettex, E., Porter, W. P. and Grémillet, D. 2013. Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. – *J. Avian Biol.* 44: 255–262.
- Gaston, A. J. and Jones, I. L. 1998. *The auks: Alcidae*. – Oxford Univ. Press.
- González-Solís, J., Croxall, J. P. and Wood, A. G. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. – *Oikos* 90: 390–398.
- Grandgeorge, M., Wanless, S., Dunn, T. E., Maumy, M., Beaugrand, G. and Grémillet, D. 2008. Resilience of the British and Irish seabird community in the twentieth century. – *Aquat. Biol.* 4: 187–199.
- Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M. and Hamer, K. C. 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. – *J. R. Soc. Interface* 15: 20180084.
- Griffiths, R., Daan, S. and Dijkstra, C. 1996. Sex identification in birds using two CHD genes. – *Proc. R. Soc. B* 263: 1251–1256.
- Halsey, L. G., Butler, P. J. and Blackburn, T. M. 2006. A phylogenetic analysis of the allometry of diving. – *Am. Nat.* 167: 276–287.
- Harris, M. P. and Wanless, S. 1984. The effect of the wreck of seabirds in February 1983 on auk populations on the Isle of May (Fife). – *Bird Study* 31: 103–110.
- Harris, M. P. and Wanless, S. 1990. Molt and autumn colony attendance of auks. – *Br. Birds* 83: 55–66.
- Harris, M. P. and Wanless, S. 1996. Differential responses of guillemot *Uria aalge* and shag *Phalacrocorax aristotelis* to a late winter wreck. – *Bird Study* 43: 220–230.
- Harris, M. P. and Wanless, S. 2011. *The PUFFIN*. – T. and A. D. Poyser.
- Harris, M. P. and Wanless, S. 2016. The use of webcams to monitor the prolonged autumn attendance of guillemots on the Isle of May in 2015. – *Scottish Birds* 36: 3–9.
- Harris, M. P., Wanless, S. and Webb, A. 2000. Changes in body mass of common guillemots *Uria aalge* in southeast Scotland throughout the year: implications for the release of cleaned birds. – *Ring. Migr.* 20: 134–142.

- Harris, M. P., Daunt, F., Newell, M., Phillips, R. A. and Wanless, S. 2010. Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. – *Mar. Biol.* 157: 827–836.
- Harris, M. P., Daunt, F., Bogdanova, M. I., Lahoz-Monfort, J. J., Newell, M., Phillips, R. A. and Wanless, S. 2013. Inter-year differences in survival of Atlantic puffins *Fratercula arctica* are not associated with winter distribution. – *Mar. Biol.* 160: 2877–2889.
- Harris, M. P., Wanless, S. and Jensen, J. K. 2014. When are Atlantic puffins *Fratercula arctica* in the North Sea and around the Faroe Islands flightless? – *Bird Study* 61: 182–192.
- Harris, M. P., Wanless, S., Ballesteros, M., Moe, B., Daunt, F. and Erikstad, K. E. 2015a. Geolocators reveal an unsuspected moulting area for Isle of May common guillemots *Uria aalge*. – *Bird Study* 62: 267–270.
- Harris, M. P., Leopold, M. F., Jensen, J. K., Meesters, E. H. and Wanless, S. 2015b. The winter diet of the Atlantic puffin *Fratercula arctica* around the Faroe Islands. – *Ibis* 157: 468–479.
- Hays, G. C., Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Martin, C., Metcalfe, J. D. and Papi, F. 2001. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. – *J. Exp. Biol.* 204: 4093–4098.
- Hedd, A., Regular, P. M., Montevecchi, W. A., Buren, A. D., Burke, C. M. and Fifield, D. A. 2009. Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. – *Mar. Biol.* 156: 741–751.
- Hedd, A., Fifield, D. A., Burke, C. M., Montevecchi, W. A., McFarlane Tranquilla, L. A., Regular, P. M., Buren, A. D. and Robertson, G. J. 2010. Seasonal shift in the foraging niche of Atlantic puffins *Fratercula arctica* revealed by stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses. – *Aquat. Biol.* 9: 13–22.
- Humphries, M. M., Umbanhowar, J. and McCann, K. S. 2004. Bioenergetic prediction of climate change impacts on northern mammals. – *Integr. Comp. Biol.* 44: 152–162.
- Hyrenbach, K. D., Fernández, P. and Anderson, D. J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. – *Mar. Ecol. Prog. Ser.* 233: 283–301.
- Jury, J. 1986. Razorbill swimming at depth of 140 m. – *Br. Birds* 79: 339.
- Kato, A., Watanuki, Y., Nishimi, I., Kuroki, M., Shaugnessy, P. and Naito, Y. 2000. Variation in foraging and parental behavior of King Cormorants. – *Auk* 117: 718–730.
- King, J. R. 1974. Seasonal allocation of time and energy resources in birds. – *Avian Energ.* 15: 4–85.
- Lenth, R. V. 2019. emmeans: estimated marginal means, aka least-squares means. – R package ver. 1.3.3, <<https://cran.r-project.org/web/packages/emmeans/>>.
- Lewis, S., Benvenuti, S., Dall’Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S. and Hamer, K. C. 2002. Sex-specific foraging behaviour in a monomorphic seabird. – *Proc. R. Soc. B* 269: 1687–1693.
- Linnebjerg, J. F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A. and Frederiksen, M. 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. – *PLoS One* 8: e72987.
- Linnebjerg, J. F., Reuleaux, A., Mouritsen, K. N. and Frederiksen, M. 2015. Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland. – *Waterbirds* 38: 143–152.
- Linnebjerg, J. F., Frederiksen, M., Kolbeinsson, Y., Snaethórsson, A. Ö., Thórisson, B. and Thórarinnsson, T. L. 2018. Non-breeding areas of three sympatric auk species breeding in three Icelandic colonies. – *Polar Biol.* 41: 1951–1961.
- Lovvorn, J. R. 2004. Stroke patterns and regulation of swim speed and energy cost in free-ranging Brunnich’s guillemots. – *J. Exp. Biol.* 207: 4679–4695.
- Martin, G. R. and Wanless, S. 2015. The visual fields of common guillemots *Uria aalge* and Atlantic puffins *Fratercula arctica*: foraging, vigilance and collision vulnerability. – *Ibis* 157: 798–807.
- McFarlane Tranquilla, L. A., Hedd, A., Burke, C. M., Montevecchi, W. A., Regular, P. M., Robertson, G. J., Stapleton, L. A., Wilhelm, S. I., Fifield, D. A. and Buren, A. D. 2010. High arctic sea ice conditions influence marine birds wintering in Low Arctic regions. – *Estuar. Coast. Shelf Sci.* 89: 97–106.
- McNamara, J. M. and Houston, A. I. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. – *Phil. Trans. R. Soc. B* 363: 301–319.
- Mori, Y. and Boyd, I. L. 2004. Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? – *Mar. Ecol. Prog. Ser.* 275: 241–249.
- Murphy, M. E. 1996. Energetics and nutrition of molt. – In: Carey, C. (ed.), *Avian Energetics and Nutritional Ecology*. Chapman and Hall, pp. 158–198.
- Ouwehand, J., Leopold, M. F. and Camphuysen, K. C. J. 2004. A comparative study of the diet of guillemots *Uria aalge* and razorbills *Alca torda* killed during the tricolor oil incident in the south-eastern North Sea in January 2003. – *Atl. Seabirds* 6: 147–164.
- Padget, O., Dell’Ariccia, G., Gagliardo, A., González-Solís, J. and Guilford, T. 2017. Anosmia impairs homing orientation but not foraging behaviour in free-ranging shearwaters. – *Sci. Rep.* 7: 9668.
- Paredes, R., Jones, I. L., Boness, D. J., Tremblay, Y. and Renner, M. 2008. Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. – *Can. J. Zool.* 86: 610–622.
- Peery, M. Z., Henkel, L. A., Newman, S. H., Becker, B. H., Harvey, J. T., Thompson, C. W. and Beissinger, S. R. 2008. Effects of rapid flight feather molt on postbreeding dispersal in a pursuit-diving seabird. – *Auk* 125: 113–123.
- Phillips, R. A., Lewis, S., González-Solís, J. and Daunt, F. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. – *Mar. Ecol. Prog. Ser.* 578: 117–150.
- Regular, P. M., Davoren, G. K., Hedd, A. and Montevecchi, W. A. 2010. Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. – *Mar. Ecol. Prog. Ser.* 415: 295–304.
- Regular, P. M., Hedd, A. and Montevecchi, W. A. 2011. Fishing in the dark: a pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. – *PLoS One* 6: e26763.
- Richard, G., Vacque-Garcia, J., Jouma’a, J., Picard, B., Genin, A., Arnould, J. P. Y., Bailleul, F. and Guinet, C. 2014. Variation in body condition during the post-moult foraging trip of southern elephant seals and its consequences on diving behaviour. – *J. Exp. Biol.* 217: 2609–2619.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. 2003. Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. – *J. Exp. Biol.* 206: 1461–1470.

- Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. 2002. Ecological and evolutionary traps. – *Trends Ecol. Evol.* 17: 474–480.
- Schreer, J. F., Kovacs, K. M. and O'Hara Hines, R. J. 2001. Comparative diving patterns of pinnipeds and seabirds. – *Ecol. Monogr.* 71: 137–162.
- Shoji, A., Elliott, K. H., Fayet, A. L., Boyle, D., Perrins, C. and Guilford, T. 2015. Foraging behaviour of sympatric razorbills and puffins. – *Mar. Ecol. Prog. Ser.* 520: 257–267.
- Shoji, A., Aris-Brosou, S., Owen, E., Bolton, M., Boyle, D., Fayet, A. L., Dean, B., Kirk, H. L., Freeman, R., Perrins, C. and Guilford, T. 2016. Foraging flexibility and search patterns are unlinked during breeding in a free-ranging seabird. – *Mar. Biol.* 163: 72.
- St John Glew, K., Wanless, S., Harris, M. P. M. P., Daunt, F., Erikstad, K. E., Strøm, H., Trueman, C. N. C. N., John Glew, K. S., Wanless, S., Harris, M. P. M. P., Daunt, F., Erikstad, K. E., Strøm, H. and Trueman, C. N. C. N. 2018. Moulting location and diet of auks in the North Sea, inferred from coupled light-based and isotope-based geolocation. – *Mar. Ecol. Prog. Ser.* 599: 239–251.
- Swennen, C. and Duiven, P. 1991. Diving speed and food-size selection in common guillemots, *Uria aalge*. – *Netherlands J. Sea Res.* 27: 191–196.
- Thaxter, C. B., Daunt, F., Hamer, K. C., Watanuki, Y., Harris, M. P., Grémillet, D., Peters, G. and Wanless, S. 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? – *J. Avian Biol.* 40: 75–84.
- Thaxter, C. B., Wanless, S., Daunt, F., Harris, M. P., Benvenuti, S., Watanuki, Y., Grémillet, D. and Hamer, K. C. 2010. Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. – *J. Exp. Biol.* 213: 1018–1025.
- Thaxter, C. B., Daunt, F., Grémillet, D., Harris, M. P., Benvenuti, S., Watanuki, Y., Hamer, K. C. and Wanless, S. 2013. Modelling the effects of prey size and distribution on prey capture rates of two sympatric marine predators. – *PLoS One* 8: e79915.
- Thompson, C. W., Wilson, M. L., Melvin, E. F., John, D. and Pierce, D. J. 1998. An unusual sequence of flight-feather in common murres and its evolutionary implications. – *Auk* 115: 653–669.
- Watanuki, Y., Wanless, S., Harris, M. P., Lovvorn, J. R., Miyazaki, M., Tanaka, H. and Sato, K. 2006. Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. – *J. Exp. Biol.* 209: 1217–1230.
- Weimerskirch, H., Barbraud, C. and Lys, P. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. – *Sour. Ecol. Evol.* 81: 309–318.
- Welcker, J., Steen, H., Harding, A. M. A. and Gabrielsen, G. W. 2009. Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. – *Ibis* 151: 502–513.
- Whitehead, T. O., Connan, M., Ropert-Coudert, Y. and Ryan, P. G. 2017. Subtle but significant segregation in the feeding ecology of sympatric penguins during the critical pre-moult period. – *Mar. Ecol. Prog. Ser.* 565: 227–236.
- Wilson, R. P. 1999. Foraging behaviour of the chinstrap penguin *Pygoscelis antarctica* at Ardley Island, Antarctica. – *Mar. Ornithol.* 27: 92–95.
- Wilson, L. J., Daunt, F. and Wanless, S. 2004. Self-feeding and chick provisioning diet differ in the common guillemot *Uria aalge*. – *Ardea* 92: 197–208.

Supplementary material (available online as Appendix jav-02012 at <www.avianbiology.org/appendix/jav-02012>). Appendix 1–4.