

Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills

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SUMMARY

Species of bird that use their wings for underwater propulsion are thought to face evolutionary trade-offs between flight and diving, leading to the prediction that species with different wing areas relative to body mass (i.e. different wing loadings) also differ in the relative importance of flight and diving activity during foraging trips. We tested this hypothesis for two similarly sized species of Alcidae (common guillemots and razorbills) by using bird-borne devices to examine three-dimensional foraging behaviour at a single colony. Guillemots have 30% higher wing loading than razorbills and, in keeping with this difference, razorbills spent twice as long in flight as a proportion of trip duration whereas guillemots spent twice as long in diving activity. Razorbills made a large number of short, relatively shallow dives and spent little time in the bottom phase of the dive whereas guillemots made fewer dives but frequently attained depths suggesting that they were near the seabed (ca. 35–70 m). The bottom phase of dives by guillemots was relatively long, indicating that they spent considerable time searching for and pursuing prey. Guillemots also spent a greater proportion of each dive bout underwater and had faster rates of descent, indicating that they were more adept at maximising time for pursuit and capture of prey. These differences in foraging behaviour may partly reflect guillemots feeding their chicks single large prey obtained near the bottom and razorbills feeding their chicks multiple prey from the water column. Nonetheless, our data support the notion that interspecific differences in wing loadings of auks reflect an evolutionary trade-off between aerial and underwater locomotion.

Key words: *Uria aalge*, *Alca torda*, optimal foraging, diving behaviour, life history, wildlife telemetry, data loggers.

INTRODUCTION

Species of bird that use their wings for underwater propulsion typically have reduced wing areas relative to body mass (higher wing loadings) (Gaston, 2004). Whilst high wing loading reduces drag and permits more effective propulsion underwater, it also lowers aerial manoeuvrability and increases energy expenditure during flight (Pennycuik, 1987; Witter and Cuthill, 1993). Thus, diving species face evolutionary trade-offs between efficient travel in air and water (Kovacs and Meyers, 2000), and so species with different wing loadings are predicted to differ in their relative use of horizontal and vertical dimensions for foraging. This prediction is broadly supported by differences in the foraging ranges and maximum dive depths of distantly-related taxa of underwater feeders that use different methods to propel themselves beneath the surface [plunge-divers compared with surface divers (Ashmole, 1971; Gaston, 2004)]. It is not clear, however, to what extent this trade-off also occurs among more closely related species that rely entirely on wing propulsion underwater. Moreover, high wing loadings in offshore and pelagic feeding birds could be an adaptation associated with maximising high-speed long-distance flight efficiency rather than improving diving ability (Lovvorn and Jones, 1994; Bridge, 2004).

Wing loading increases with body size (Calder, 1984), and members of the family Alcidae (auks) have high wing loadings for their size [fig. 3.8 in Gaston (Gaston, 2004)], reflecting their reliance on wing propulsion during dives (Gaston and Jones, 1998). Among auks, common guillemots *Uria aalge* (Pontoppidan) (hereafter guillemots) and razorbills *Alca torda* L. often occur in mixed colonies and are similar in size [e.g. wing length: guillemot ca. 196–218 mm, razorbill ca. 201–216 mm; tarsus length: guillemot ca. 38–40 mm, razorbill ca. 33–37 mm (Gaston and Jones 1998)]. However, guillemots have ca. 30% higher wing loading than razorbills (Pennycuik, 1997; Hipfner and Chapdelaine, 2002), leading to the prediction that guillemots make greater use of the vertical dimension for foraging whereas razorbills make greater use of the horizontal dimension through flight. In keeping with this prediction, dives by guillemots appear to be typically longer and deeper than those by razorbills (Paredes et al., 2008; Thaxter et al., 2009). However, there are only limited comparative data on horizontal movements (Wanless et al., 1990), and no previous study has compared horizontal and vertical movements for the two species at a single colony.

During diving activity, birds alternate periods underwater with periods on the surface replenishing oxygen stores and eliminating

carbon dioxide from the body in preparation for the next dive (Enstipp et al., 2001; Halsey and Butler, 2006). Birds can increase time available for pursuit and capture of prey by increasing both time underwater during a dive bout and rates of transit between the surface and depths where prey are located (Houston and Carbone, 1992; Walton et al., 1998). Descending too quickly, however, could reduce efficiency by depleting oxygen reserves and hence reducing time available for pursuit of prey. The relationship between dive and pause durations, together with the vertical speeds attained by birds during dives to different depths, thus provide important information on how effectively birds use the vertical dimension for foraging (Watanuki et al., 2006; Cook et al., 2008).

Here, we use a variety of bird-borne activity loggers to provide detailed information on the three-dimensional foraging movements and behaviour of guillemots and razorbills at the same colony, where the two species exploit similar prey [mainly sandeels *Ammodytes marinus* and sprats *Sprattus sprattus* (Wilson et al., 2005; Thaxter et al., 2009)]. We test the hypothesis that these species make contrasting use of the potential foraging environment around the colony by examining three related predictions: (1) razorbills spend longer in flight than guillemots and sample more of the horizontal dimension; (2) guillemots spend longer in diving activity than razorbills and sample more of the vertical dimension; and (3) guillemots spend a greater proportion of time underwater during dive bouts and have faster vertical travel speeds than razorbills, associated with maximising time in search and pursuit of prey at depth.

MATERIALS AND METHODS

Bird-borne instruments

Fieldwork took place between 1999 and 2006 at a large mixed colony of guillemots and razorbills (Wilson et al., 2005) on the Isle of May, SE Scotland (56°11'N, 2°33'W). Data were collected each year except 2000, 2004 and 2006 for guillemots, and 2000–2001 and 2004 for razorbills. Adults with 1–2-week-old chicks ($N=71$ guillemots, $N=20$ razorbills) were captured at the breeding site using an 8 m telescopic pole with a noose or crook and equipped with one of two types of activity logger. Different birds were used each year, only one member of a pair was tagged and only one device was deployed per bird. To study horizontal movements at sea, locations of dives and time activity budgets, an activity logger was attached to the central back feathers, with successful deployments achieved for 30 guillemots and 14 razorbills. These were of three types: (1) compass loggers, Earth and Ocean Technologies, Kiel, Germany (14.5 g), (2) direction recorders, Istituto di Elaborazione dell'Infomazione (IEI), Pisa, Italy (25 g), and (3) event recorders, IEI (28 g). Compass loggers recorded directional information *via* two perpendicular compass vector sensors (directional resolution within 0.1°) plus temperature (resolution within 0.1°C, range 0–20°C) and time and date at 1–2 s intervals. Direction recorders recorded orientation of birds during flight with respect to magnetic north *via* a compass and a flight sensor (small microphone), both sampling at 6 s intervals (Benvenuti et al., 1998; Benvenuti et al., 2001; Dall'Antonia et al., 2001). Event recorders recorded flight activity using the same flight sensor as above, and diving behaviour using a depth metre (resolution 0.3 m, range 0–70 m) sampling at 4 s intervals (Benvenuti et al., 1998; Benvenuti et al., 2001; Dall'Antonia et al., 2001).

To study vertical dive depths and use of the water column, a time-depth recorder (TDR) was attached to the underbelly or back feathers of a separate sample of 47 guillemots and 11 razorbills. Only one logger was attached per bird. TDRs were of four types:

(1) PreciTD, Earth and Ocean Technologies (23 g); (2) Lotek TDR, Lotek Wireless, St John's, Newfoundland, Canada (5 g); (3) FPBS-82A, Fujikura, Tokyo, Japan (16 g); and (4) IEI TDR (28 g). All TDRs recorded depth to the nearest 0.01 m at a sampling interval of 1–4 s. IEI TDRs were housed within event recorders, and were hence carried on the same birds.

Devices were attached with waterproof tape (Tesa AG, Hamburg, Germany), allowing loss through feather moult if not retrieved. Attachment took <15 min, after which birds were released to the breeding site. Birds were recaptured after 1–10 days (usually 2 days) and the logger was removed. Birds typically returned to the breeding site and resumed normal brooding behaviour within 15 min of being released, and no chick was lost during the period of deployment. Devices weighed 2–4% of body masses of guillemots (mean body mass=907±55 g, $N=25$) and 3–4% of body masses of razorbills (600±87 g, $N=15$). In previous studies, loggers up to 27 g had no discernible impacts on foraging, breeding site attendance or food delivery to chicks of either species (e.g. Monaghan et al., 1994; Benvenuti et al., 2001; Tremblay et al., 2003), although some adverse effects have been detected using other devices (Hamel et al., 2004; Paredes et al., 2005). In this study, time spent at the colony during daylight hours did not differ between individuals with loggers and unequipped controls either for guillemots (11.1±2.7 h and 10.7±3.9 h, respectively; GLM with year as a fixed effect and bird identity as a random effect; $F_{1,40}=0.1$, $P=0.8$) or for razorbills (10.0±3.7 h and 10.7±2.5 h, respectively; $F_{1,16}=0.4$, $P=0.6$).

Manipulation of data

Data from activity loggers were downloaded to a computer and processed using Multitrace-Route 6.0 software (Jensen Software Systems, Laboe, Germany). Four activities could be distinguished (Benvenuti et al., 2001; Dall'Antonia et al., 2001; Thaxter et al., 2009): (1) site attendance, characterised by a stable compass signal; (2) flight, recognised by low amplitude oscillation; (3) time on the sea surface, identified by noisy compass signals and stable temperature; and (4) diving, characterised by repeated changes in pitch as birds upended when they dived underwater and then resurfaced at the end of the dive. Trip durations determined from these data closely matched observed periods of absence from the breeding site (Thaxter et al., 2009), and our interpretation of logger traces closely matched other studies using similar devices (e.g. Ropert-Coudert et al., 2004).

Durations of foraging trips were calculated from the time of the first flight activity as the bird left the colony until the time of the last flight activity as it returned. The frequency and durations of dives were calculated for each trip, and the total time spent in diving activity was calculated as the summed duration of dives plus pauses on the sea surface between dives (Sibley et al., 1990; Halsey et al., 2007). Tracks of birds carrying compass and directional loggers were reconstructed by combining data on direction of travel during each period of flight and duration of flight period following previous authors (Benvenuti et al., 2001; Daunt et al., 2002) and assuming a mean flight speed of 19.1 m s⁻¹ for guillemots and 16.0 m s⁻¹ for razorbills (Pennycuik, 1997). Different species of birds have characteristic flight speeds, with wing loading and phylogeny together explaining most of the variation in airspeed across a wide range of species (Allerstam et al., 2007). We are therefore confident that these data provided a robust basis for reconstructing foraging tracks in our study. Directions of travel were corrected for wind speed and direction (sampled hourly) using data from Leuchars, ca. 20 km from the Isle of May (<http://www.badc.nerc.ac.uk/home/>). An endpoint correction was then applied to constrain tracks to start and finish at the same location (for details, see Daunt et al., 2005).

Locations of dives at sea were examined in Arc-View GIS, and the total area that birds of each species used for diving was compared using fixed kernel density estimates with least-squares cross-validation (Worton, 1989; Magalhães et al., 2008) Following previous authors (e.g. Hamer et al., 2007) the 95% and 50% fixed kernel density estimates were taken to represent the area of active use and core foraging area, respectively. In addition, we used distance of the furthest dive from the colony as an estimate of foraging range, and distance from the nearest point on the mainland to estimate the extent to which birds were feeding inshore or offshore of the breeding colony. We also calculated the total distance travelled on each trip by summing distances between successive time steps (1–2 s) when the bird was in flight.

Data from TDRs were analysed using Multitrace Dive (Jensen Software Systems) and specialist software (A. Ribolini, unpublished) to determine both the duration and the maximum depth attained for all dives deeper than 1 m (shallower dives often occur during bathing or other activities not associated with foraging, and so were excluded from analysis). Dives were also split into bouts (periods of sustained diving activity) following Sibly et al. (Sibly et al., 1990). To compare how efficiently birds of each species made use of time during diving activity, we examined the relationship between total time spent underwater and total time spent in surface pauses during each dive bout (Walton et al., 1998; Cook et al., 2008). We also

examined the minimum pause duration associated with individual dives of different durations, as a measure of maximum efficiency during an individual dive cycle (defined as a dive plus its preceding surface pause). To compare rates of transit between the surface and the bottom of the dive (Benvenuti et al., 2001; Watanuki et al., 2006), we examined the relationship between dive depth and both mean and maximum vertical descent speeds. In addition, we calculated time spent at the bottom of each dive, presumed to represent time spent searching for and pursuing prey (Halsey et al., 2007; Elliott et al., 2008a). This bottom phase was defined as occurring when vertical speed was $\leq 0.2 \text{ m s}^{-1}$ within 40% of maximum dive depth. To quantify differences between species in the profiles of dives, we calculated a time allocation at depth (TAD) index, following Fedak et al. (Fedak et al., 2001), as:

$$\text{TAD index} = \left[\frac{\sum_{i=2}^N [(d_i + d_{i-1}) / 2] \times t - (D^2/S)}{(D \times T) - 2(D^2/S)} \right],$$

where d =depth readings from the TDR throughout the dive, i =sequence of depth readings during the dive, t =sampling time interval, D =maximum depth reached during the dive, T =dive duration, and S =mean rate of change of depth. The time allocation at depth index is close to 0.5 for V-shaped dives with little time spent at the bottom of the dive and approaches 1.0 for U-shaped dives (Fedak et al., 2001; Elliott et al., 2008b).

Table 1. Foraging behaviour of guillemots and razorbills

	Guillemot (means \pm s.d.)	Razorbill (means \pm s.d.)	<i>P</i>
Overall characteristics of trips			
Trip duration (h)	8.3 \pm 6.6	5.1 \pm 5.6	**
Total time:			
in flight (h)	0.6 \pm 0.4	0.8 \pm 0.7	*
on sea surface (h) [†]	5.1 \pm 5.9	3.1 \pm 4.1	*
diving activity (h)	2.9 \pm 1.9	1.5 \pm 1.8	**
Of which:			
underwater (h)	1.9 \pm 1.3	0.8 \pm 0.7	**
surface pauses (h)	0.9 \pm 0.6	0.5 \pm 0.5	*
Proportion of time:			
in flight (%)	10.3 \pm 8.0	21.2 \pm 16.6	***
underwater (%)	28.8 \pm 9.5	17.5 \pm 10.6	*
Horizontal movements			
Horizontal distance travelled (km trip ⁻¹)	34.5 \pm 29.8	47.8 \pm 45.5	
Flight sinuosity index	0.16 \pm 0.10	0.27 \pm 0.15	
Maximum distance from colony (km)	14.4 \pm 12.2	18.4 \pm 14.8	
Vertical movements			
Number of dives trip ⁻¹	94 \pm 83	142 \pm 169	**
Vertical distance travelled (km trip ⁻¹)	4.8 \pm 3.4	1.5 \pm 1.5	***
Time in bottom phase (s dive ⁻¹)	30.7 \pm 22.0	5.7 \pm 7.1	***
Dive:pause ratio during dive bouts	2.0 \pm 1.0	1.7 \pm 1.1	*
Individual dive:pause ratio	2.2 \pm 1.3	1.8 \pm 1.7	**
Shallow dives			
Depth (m)	13.4 \pm 8.9	6.5 \pm 5.2	***
Duration (s)	46.4 \pm 27.4	23.1 \pm 14.9	***
Time allocation at depth index	0.68 \pm 0.15	0.55 \pm 0.13	***
Mean rate of descent (m s ⁻¹)	0.93 \pm 0.41	0.64 \pm 0.27	***
Mean rate of ascent (m s ⁻¹)	0.83 \pm 0.38	0.64 \pm 0.29	***
Deep dives			
Depth (m)	50.4 \pm 7.4	–	
Duration (s)	118.4 \pm 17.2	–	
Time allocation at depth index	0.88 \pm 0.10	–	
Mean rate of descent (m s ⁻¹)	1.38 \pm 0.16	–	
Mean rate of ascent (m s ⁻¹)	1.32 \pm 0.22	–	

Significance levels: *** P <0.001, ** P <0.01, * P <0.05 and blank=no significant difference between species. [†]Excluding surface pauses within dive bouts. Data are means per trip for horizontal movements (N =81 trips from 30 guillemots and 76 trips from 14 razorbills) and means per dive for vertical movements (N =9065 dives from 47 guillemots and 5426 dives from 11 razorbills). Dive depth; duration; time allocation at depth index; and rates of descent and ascent are given separately for shallow dives (up to ca. 30 m) and deep dives (ca. 32–70 m).

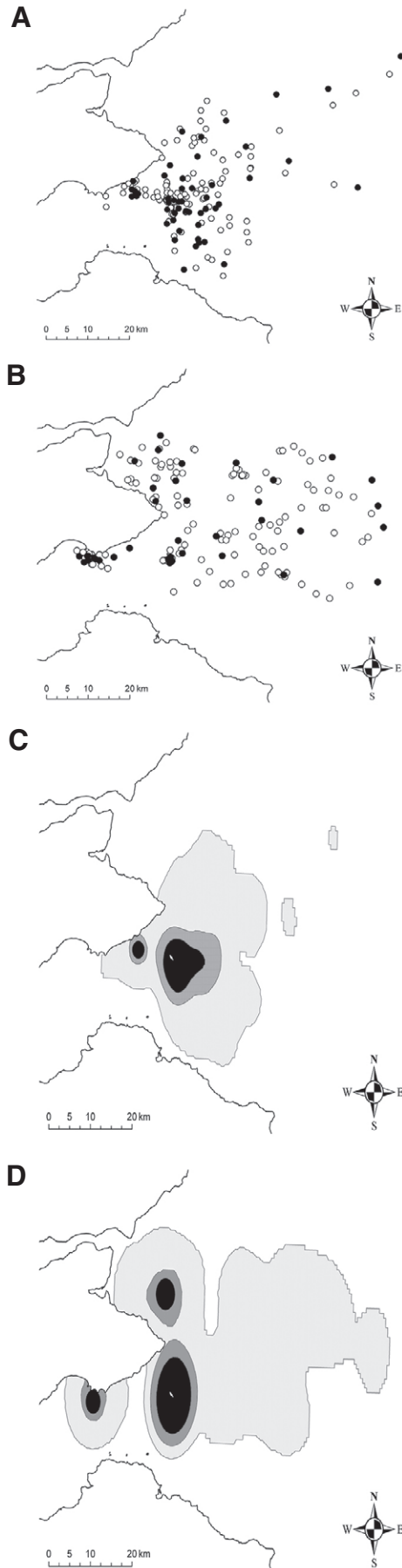


Fig. 1. (A,B) Locations at sea (open symbols) and destinations of foraging trips (solid symbols) of (A) guillemots and (B) razorbills from the Isle of May. (C,D) Kernels encompassing 50% (dark grey), 75% (medium grey) and 95% (light grey) of diving locations of (C) guillemots and (D) razorbills.

Statistical analyses

We used general linear mixed effects models (GLMs) and generalised linear mixed models (GLMMs) for data with normal and with Poisson or binomial error distributions, respectively. To account for cases where more than one foraging trip was recorded per bird, bird identity was included as a random effect. Proportions were arc-sine transformed prior to analysis. To account for possible serial autocorrelation of variables relating to diving behaviour, a continuous autoregressive correlation structure was included (Beck et al., 2003; Thaxter et al., 2009), with time of day (22:01–04:00 h; 04:01–10:00 h; 10:01–16:00 h; 16:01–22:00 h) included as a fixed effect. All GLMs used F -tests and GLMMs used χ^2 tests to assess the significance of effects and interactions. Means are presented as ± 1 standard deviation unless otherwise stated. All analyses were performed using R Version 2.9.0 (R Development Core Team, 2009).

RESULTS

Horizontal movements

We recorded 81 foraging trips from 30 guillemots and 76 foraging trips from 14 razorbills. Trips by guillemots were 3.2 h longer on average than trips by razorbills but razorbills spent significantly longer in flight per trip, both in total and as a proportion of trip duration (Table 1). However, because of the slower mean flight speed in razorbills (Pennycuik, 1997), there was no significant difference between species in foraging range or estimated total distance travelled per trip (Table 1). Nonetheless, the overall foraging area (95% fixed kernel density for locations of dives) was twice as large for razorbills as for guillemots (2201 km² and 1094 km², respectively), and the core foraging area (50% fixed kernel density) was 85% larger for razorbills than for guillemots (155 km² and 84 km², respectively; Fig. 1). This corresponded to a significant difference in the extent to which birds travelled offshore; for razorbills, almost half of all trips were within 10 km of the coast, mainly inshore of the Isle of May with most of the remainder to areas 30–40 km offshore. By contrast, for guillemots, 60% of trips were to areas 10–20 km from the coast and slightly offshore of the colony, with birds making little use of areas closer to the coast or more than 25 km from the coast (Fig. 2; Kolmogorov–Smirnov two-sample test; $Z=0.34$, $P<0.05$). The bimodal frequency distribution for razorbills was not due to individual specialisation in trip locations because most birds (67%) used both offshore and inshore locations.

Diving behaviour

Guillemots made fewer dives per trip than razorbills but spent a significantly larger proportion of each trip underwater (Table 1; $F_{1,28}=4.6$, $P<0.05$). In terms of overall vertical distance travelled underwater during a trip, guillemots travelled nearly three times further on average than razorbills (Table 1). Guillemots also spent 5–6 times longer than razorbills at the bottom of each dive (Table 1), suggesting a much greater time spent searching for and pursuing prey at depth. Time spent in diving activity (including surface pauses) increased linearly with flight duration for both species (Fig. 3) but at a significantly faster rate for guillemots ($F_{1,104}=7.94$, $P<0.01$), resulting in much longer time in diving activity per unit

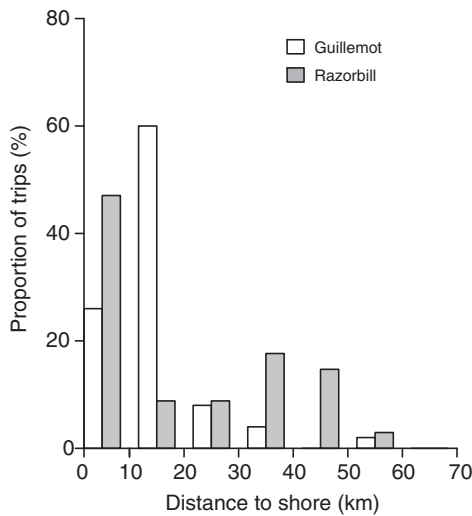


Fig. 2. Frequency distribution of distance from shore of dive furthest from colony on each trip for guillemots and razorbills.

time in flight for guillemots than for razorbills (3.57 ± 2.94 and 1.40 ± 1.26 , respectively; $F_{1,31}=12.6$, $P<0.01$). There was a similar difference between species in the relationship between time spent underwater and time in flight ($F_{1,75}=12.0$, $P<0.001$). Time spent in diving activity was also strongly correlated with total vertical distance travelled underwater for both species ($R=0.92$ and 0.94 , respectively).

Guillemots had significantly higher dive:pause ratios than razorbills in terms of both the total duration of dives and pauses during dive bouts and the minimum pauses associated with individual dives of different durations (Table 1). There was a significant positive relationship between time spent underwater and in surface pauses during a dive bout (Fig. 4A) and so this difference in dive:pause ratios could have resulted simply from guillemots making longer dives on average. However, this was not the case; the slope of the linear relationship following square-

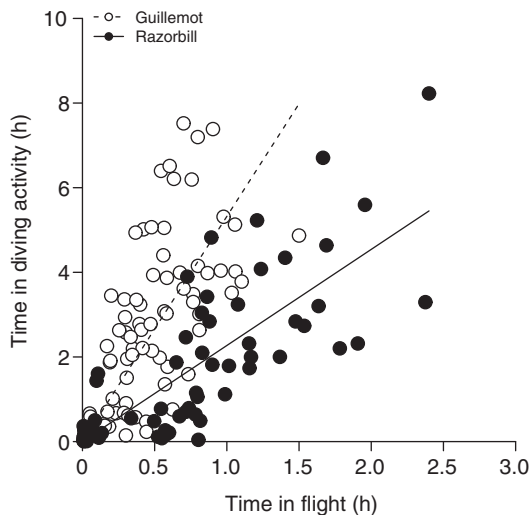


Fig. 3. Relationship between time in flight and time in diving activity during trips by guillemots and razorbills. Best fit regression equations are: guillemot, time (h) diving = 5.32 (s.e.m. ± 0.32) \times time (h) in flight; razorbill, time (h) diving = 2.27 (s.e.m. ± 0.41) \times time (h) in flight.

root transformation was significantly steeper for guillemots ($\beta=1.06 \pm 0.02$) than for razorbills ($\beta=0.92 \pm 0.05$; $F_{1,936}=7.0$, $P<0.01$; Fig. 4A), indicating that for a given time spent in surface pauses, guillemots spent significantly longer underwater than razorbills. Similarly, the relationship between individual dive duration and minimum preceding pause duration was significantly steeper for guillemots ($\beta=0.540 \pm 0.026$) than for razorbills ($\beta=0.387 \pm 0.047$; $F_{1,240}=10.5$, $P<0.01$; Fig. 4B), suggesting that guillemots had a lower requirement for surface pauses during individual dive cycles.

Razorbills did not dive beyond 32 m depth whereas for guillemots the frequency distributions of dive depth and duration were bimodal (Fig. 5) with a clear separation between short shallow dives ($\leq ca.$ 30 m) and long deep dives ($ca.$ 30–70 m). Deep dives by guillemots comprised a greater proportion of time underwater than shallow dives (Fig. 5). There was a significant difference in durations and time allocation at depth indices of deep and shallow dives by guillemots (GLM, $F_{1,3761}=593.2$, $P<0.001$ and $F_{1,2386}=467.7$, $P<0.001$, respectively; Table 1). In addition, shallow dives by guillemots were deeper, of longer duration and more U-shaped (as

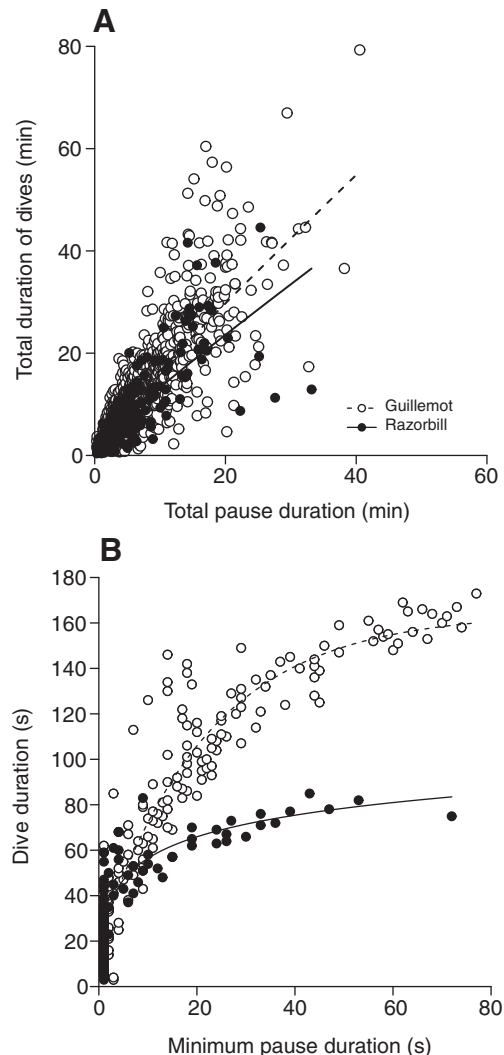


Fig. 4. Relationship between (A) total time underwater and total duration of surface pauses during a dive bout and (B) duration of individual dives and minimum duration of preceding pause for guillemots and razorbills.

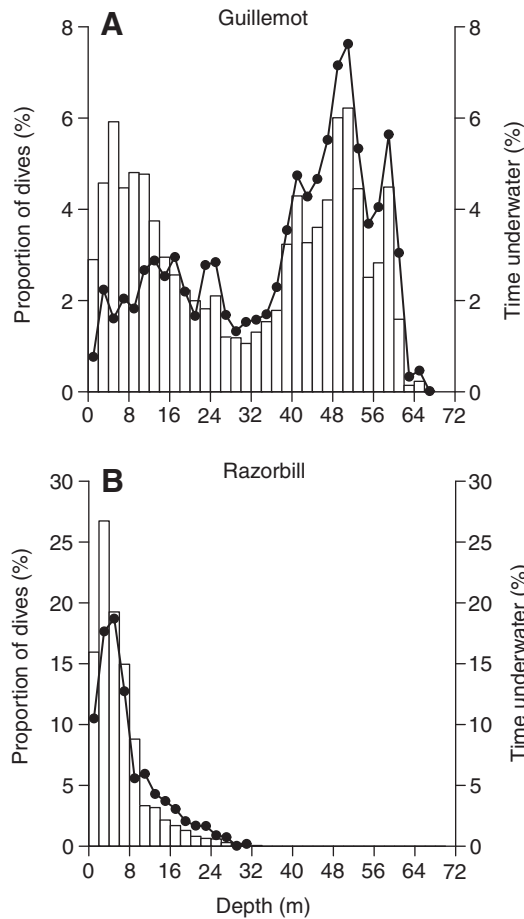


Fig. 5. Proportion of dives to different depths (\square) and proportion of time spent at different depths (\bullet) by guillemots (A) and razorbills (B).

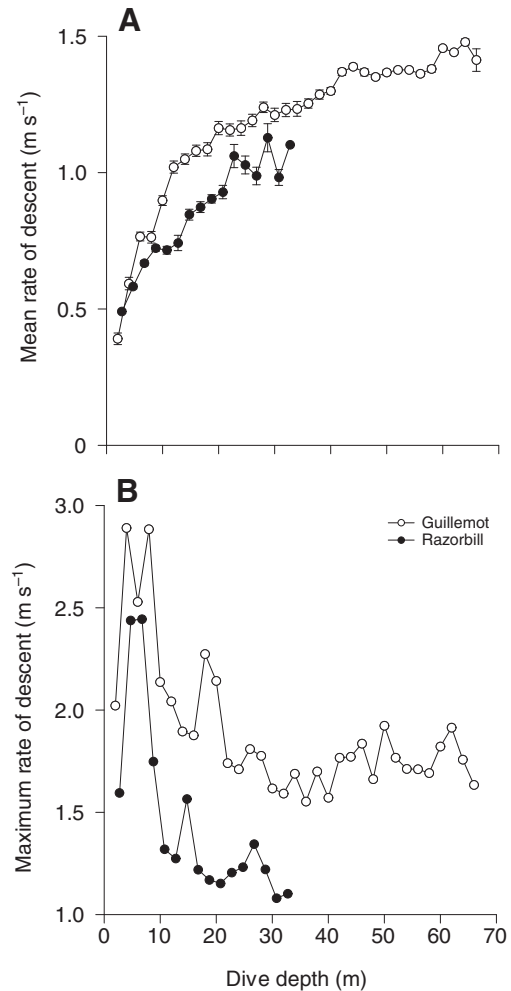


Fig. 6. Relationship between (A) mean and (B) maximum rate of descent and dive depth for guillemots and razorbills.

indicated by a higher mean time allocation at depth index) than shallow dives by razorbills (Table 1). Mean rates of vertical descent and ascent during dives were also significantly faster in guillemots than in razorbills during shallow dives ($\leq ca. 30$ m, Table 1; descent: $F_{1,50}=37.9$, $P<0.001$; ascent: $F_{1,50}=29.2$, $P<0.001$) and in guillemots during deep dives compared with shallow dives (Table 1; both tests $P<0.001$). Overall, there was a marked effect of dive depth on both mean and maximum rates of descent (Fig. 6) but there was a significant difference between species in both relationships (Fig. 6; $F_{1,45}=5.0$, $P<0.05$ and $F_{1,47}=7.6$, $P<0.01$, respectively), indicating that for any given dive depth, guillemots had faster mean and maximum rates of descent than razorbills.

DISCUSSION

This study has shown contrasting foraging behaviour in two closely related species of auk rearing chicks at the same colony. Foraging behaviour will to some extent reflect prey availability around a colony (Monaghan et al., 1994; Davoren, 2000) but our data were recorded over a similar period of years encompassing a similar range of conditions and so should provide a robust comparison between species. We found that razorbills spent more time in flight during trips whereas guillemots spent longer underwater (Table 1). Moreover, guillemots spent longer in diving activity than razorbills

per unit time in flight (Fig. 3), supporting our predictions based on the difference between species in wing loading. It has been suggested that high wing loadings of auks may not increase the effectiveness of wing propulsion underwater, because distance moved per stroke during dives by guillemots and tufted puffins *Fratercula cirrhata* decreased following a moult-induced reduction in wing area (Bridge, 2004). However, this decrease was due to a reduction in stroke duration and was accompanied by an increase in stroke frequency [fig. 4 in Bridge (Bridge, 2004)]. There was no effect of moult on speed or mechanical cost of transport ($\text{Jkg}^{-1}\text{m}^{-1}$) underwater, which suggests that feather moult resulted in a change in stroke pattern rather than a reduction in the effectiveness of wing propulsion. Our data do not represent maximum capabilities in terms of foraging ranges or dive depths. Both species have been observed carrying fish >150 km from the nearest breeding colony (Gaston and Jones, 1998), and razorbills have been recorded diving to depths of at least 120 m and guillemots to 180 m (Piatt and Nettleship, 1985). Rather, our results indicate a marked difference between species in the relative importance of flight and diving activity during foraging trips. Two-species comparisons of this type should be viewed with some caution when they are based on few metrics (Garland and Adolph, 1994). However, our multiple measurements of flying and diving ability produced a consistent pattern and so we are confident

that they provide strong support for an evolutionary trade-off between aerial and underwater locomotion.

A study at the Isle of May in the late 1980s, based on small sample sizes and using VHF telemetry, concluded that foraging ranges of razorbills were greater than those of guillemots (Wanless et al., 1990). However, this was not the case in our study; whilst razorbills spent longer in flight than guillemots, this difference was offset by their 20% slower flight speed (Pennycuik, 1997), and we found no difference between species in either foraging range or distance travelled per trip. Both species had relatively direct flight paths to and from the furthest diving location; the total distance travelled was only 20% higher than expected from direct flight in a straight line between the colony and feeding area for guillemots and 32% higher for razorbills (calculated from data in Table 1). Thus, the two species also had similar maximum foraging ranges. However, razorbills had much larger core and total foraging areas than guillemots at the population level (Fig. 1). In addition, individual razorbills foraged both inshore of the colony <10 km from the coast and offshore of the colony >30 km from the coast whereas guillemots foraged predominantly slightly offshore of the colony and 10–20 km from the coast (Fig. 2), in agreement with a previous distribution of foraging locations at the same colony (Wanless et al., 1990). These data suggest that, in addition to spending longer in flight per trip, razorbills used a greater variety of foraging locations than guillemots.

Guillemots spent longer underwater and, in keeping with previous data from VHF telemetry (Wanless et al., 1988), they also had significantly higher dive:pause ratios than razorbills (Table 1), suggesting that guillemots made more efficient use of time during diving activity for search and pursuit of prey. This difference was not due to allometry with body mass, because dive:pause ratio is mass invariant (Halsey et al., 2006; Stephens et al., 2008). Nor was it the result of guillemots making dives of longer duration, because guillemots had shorter pauses than razorbills for a given dive duration, both at the level of individual dives and of dive bouts (Fig. 4). In addition, the mean rate of vertical descent of guillemots was 1.8 times faster than that of razorbills (Table 1). Partly as a consequence of this difference, guillemots travelled 3.2 times the vertical distance travelled by razorbills despite only spending 2.4 times longer underwater (Table 1), suggesting that guillemots were much more effective than razorbills at reducing transit time between the surface and the location of prey.

Buoyancy decreases rapidly with increasing depth to about 20–30 m and much more slowly thereafter, with the change from positive to negative buoyancy in guillemots estimated to occur at about 60–70 m (Lovvorn et al., 2004). In our study, there was a positive relationship between dive depth and mean rate of descent in both species (Fig. 6), as also found previously for razorbills (Benvenuti et al., 2001), presumably reflecting a progressive decrease in the proportion of time spent at depths above 20 m where work against buoyancy is greatest (Lovvorn et al., 1999; Watanuki et al., 2003). In contrast to the mean rate of descent, however, maximum rate of descent generally decreased with increasing depth beyond ca. 5 m (Fig. 6), presumably as birds adjusted maximum swim speeds to reduce costs of travel per unit distance during deeper dives (Culik et al., 1994; Halsey and Butler, 2006). Over the range of depths where the two species overlapped, guillemots had consistently faster rates of both descent and ascent than the razorbills, indicating that the differences between species in vertical travel speeds were not simply a consequence of differences in depths attained during dives. Coinciding with their slower rates of descent and ascent, razorbills also exploited a much narrower range of depths

for foraging (Fig. 5). Previous studies also recorded that razorbills seldom dived beyond 35 m (Benvenuti et al., 2001; Dall'Antonia et al., 2001; Paredes et al., 2008), which suggests that although razorbills are clearly capable of diving deeper (Piatt and Nettleship, 1985) they may not typically do so.

The comparison of diving behaviour suggests that the two species used different methods for catching prey. Razorbills made a large number of short, relatively shallow dives and spent little time in the bottom phase of the dive whereas guillemots made fewer dives but frequently attained depths suggesting that they were near the seabed [ca. 70 m depth (UK Hydrographic Office, 1999)]. The bottom phase of dives by guillemots was also relatively long, indicating that they spent much time searching for and pursuing prey. The difference between species in diving behaviour may be particularly great during the chick-rearing phase, when our data were collected, because of differences in how prey are transported back to the brood. Guillemots are obligate single prey-loaders, returning with a single fish carried lengthways in the bill whereas razorbills are facultative multiple prey-loaders, capable of carrying a number of fish crossways in the bill (Harris and Wanless, 1985; Harris and Wanless, 1986; Gaston and Jones, 1998). As a consequence, guillemots are likely to spend time searching for a large item to bring back to the chick whereas razorbills are less constrained because they can potentially take back several small items, and so the contrast between self feeding and chick provisioning is likely to be less marked in razorbills. In keeping with this notion, Thaxter et al. (Thaxter et al., 2009) found that dives by guillemots during the final bout of each trip were 30% longer than those in preceding bouts [as also recorded in Brünnich's guillemots *Uria lomvia* (Jones et al., 2002)], probably due to greater selectivity in prey captured for the chick than for self-feeding. Guillemots may thus, to some extent, have used shallow dives to obtain prey for themselves and deep dives to obtain prey for their chick. However, the latter may also have been used for the parent's benefit, because some foraging trips by guillemots included only deep dives.

Fish schooling within the water column are likely to be more mobile than those associated with a particular area of seabed, and hence to have more variable and less predictable distributions. The lower wing loadings of razorbills may thus be associated with a requirement to spend longer in flight than guillemots, visiting a greater variety of different locations in search of such mid-water prey. By contrast, guillemots spent less time in flight but more time searching for prey underwater. Our data thus strongly support the notion that interspecific differences in wing loadings of auks reflect an evolutionary trade-off between aerial and underwater locomotion.

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