

# Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills

Rosana Paredes, Ian L. Jones, Daryl J. Boness, Yann Tremblay, and Martin Renner

**Abstract:** At the Gannet Islands, Labrador, sympatric thick-billed murres (*Uria lomvia* (L., 1758)) and razorbills (*Alca torda* L., 1758) are slightly sexually dimorphic and have similar intersexual differences in parental roles; females are the main meal providers and males are mostly involved in brooding and chick defence at the breeding site and at sea. The question is whether differences in parental roles influence the foraging behaviour patterns of males and females. Murre females foraged during twilight periods and dived shallower than males. In razorbills, although sex differences were not as clear, females also tended to dive shallower (<10 m) and more often at twilight. Males of both species foraged during daylight hours and tended to dive deeper than females. Females of both species had shorter dive bouts (i.e., duration of a series of dives) even though the number of bouts and dives per day were equal between sexes. In both species, female dives were mostly shallower W-shaped dives, likely for capturing crustaceans at twilight. In contrast, males performed mostly deeper U-shaped dives for capturing mid-water species (e.g., capelin, *Mallotus villosus* (Müller, 1776)). Altogether, our results show that the two sympatric auks had relatively similar intersexual segregation in feeding time, depth, and prey. Sex differences in nest attendance, driven by differences in parental roles, seem to explain these findings.

**Résumé :** Aux îles Gannet, Labrador, les guillemots de Brünnich (*Uria lomvia* (L., 1758)) et les petits pingouins (*Alca torda* L., 1758) qui vivent en sympatrie ont un faible dimorphisme sexuel et des différences sexuelles semblables dans leurs rôles parentaux; les femelles sont les principales approvisionneuses et les mâles sont surtout impliqués dans la couvaison et la défense des poussins au site de nidification et en mer. La question est de savoir si les différences de rôles parentaux affectent les patrons comportementaux de quête alimentaire des mâles et des femelles. Les guillemots femelles recherchent leur nourriture dans les périodes de demi-jour et plongent moins profondément que les mâles. Bien que les différences sexuelles ne soient pas aussi nettes chez les pingouins, les femelles ont aussi tendance à plonger moins profondément (<10 m) et plus souvent au demi-jour. Les mâles des deux espèces recherchent leur nourriture durant les heures de jour et tendent à plonger plus profondément que les femelles. Les femelles des deux espèces ont des épisodes de plongée (c'est-à-dire, les durées des séries de plongées) plus courts, quoique les nombres d'épisodes et de plongées soient les mêmes en une journée chez les deux sexes. Chez les deux espèces, les plongées des femelles suivent un trajet en W généralement moins profond, vraisemblablement pour capturer des crustacés au demi-jour. Au contraire, les mâles font surtout des plongées en U plus profondes pour capturer les espèces des profondeurs intermédiaires (par ex., le capelan, *Mallotus villosus* (Müller, 1776)). Dans leur ensemble, nos résultats montrent que les deux alcidés sympatriques possèdent la même ségrégation entre les sexes en ce qui a trait au moment et à la profondeur de leur alimentation, ainsi qu'en ce qui concerne les proies utilisées. Les différences de temps passé au nid, reliées aux différences des rôles parentaux, semblent expliquer ces résultats.

[Traduit par la Rédaction]

## Introduction

According to niche theory, species coexisting at equilibrium must partition the resources of their environment until interspecific competition becomes less significant than intraspecific competition (Hutchinson 1978; Ricklefs 1990). In seabirds, empirical evidence indicates partitioning of food

resources occurs in related sympatric species by habitat, prey choice (McGinnis and Emslie 2001; Day et al. 2003), and foraging times (Lance and Thompson 2005). Other studies have shown that sexes can also differ in their foraging niches, which may reduce intraspecific competition for food resources (Casaux and Barrera-Oro 2006; Breed et al. 2006). Sex differences in foraging behaviour in some marine mam-

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imals (gray seals, *Halichoerus grypus* (Fabricius, 1791): Beck et al. 2003; New Zealand fur seals, *Arctocephalus forsteri* (Lesson, 1828): Page et al. 2005; killer whales, *Orcinus orca* (L., 1758): Baird et al. 2005) and seabirds (fairy penguins, *Eudyptula minor* (J.R. Forster, 1781): Bethge et al. 1997; Adelie penguins, *Pygoscelis adeliae* (Hombron and Jacquinot, 1841): Clarke et al. 1998; diving seabirds: Bearhop et al. 2006; king cormorants, *Phalacrocorax atriceps* King, 1828: Kato et al. 2000; Japanese cormorants, *Phalacrocorax capillatus* (Temminck and Schlegel, 1850): Ishikawa and Watanuki 2002; Crozet shags, *Phalacrocorax melanogenensis* (Blyth, 1860): Cook et al. 2007; thick-billed murre, *Uria lomvia* (L., 1758): Jones et al. 2002) is explained by sexual size dimorphism (i.e., body mass and bill size; see review by Halsey et al. 2006). The larger sex is able to forage over greater distances and to deeper sections of the water column (Weimerskirch et al. 1997; Kato et al. 2000; Ishikawa and Watanuki 2002; Weimerskirch et al. 2006; Zavalaga et al. 2007). They may also forage on larger prey (Cook et al. 2007). Sex differences in foraging behaviour, however, have also been found in several monomorphic seabird species (Bethge et al. 1997; Lewis et al. 2002; Jones et al. 2002; Peck and Congdon 2006), which suggests that other factors can explain the differences found between males and females.

Thick-billed murre (henceforth murre) and razorbill (*Alca torda* L., 1758) are slightly sexually dimorphic, mostly in bill dimensions (Gaston and Jones 1998; review by Gaston and Hipfner 2000; Grecian et al. 2003). These alcids are wing-propelled divers with distinct foraging strategies; murre is a single loader (deliver a single prey held longwise in the bill) and mid-deep water divers, while razorbills are multiple loaders (deliver multiple prey held crosswise in bill) and shallow to mid-water divers (Gaston and Jones 1998). Regardless of the differences in foraging tactics, murre and razorbill males and females share similar partitioning in parental roles — biparental care is provided at the breeding site for 2 weeks and unipaternal care at sea for 3–4 weeks (Gaston and Jones 1998). At the Gannet Islands, Labrador, females are the main meal providers, while males are mostly involved in brooding and chick defence (Paredes et al. 2006). The intriguing question is whether these patterns in parental behaviour determine the foraging and diving behaviour of males and females. In other monomorphic or slightly dimorphic seabirds, the sex with the shorter foraging trip also feeds the chick more frequently (Gray and Hamer 2001; Peck and Congdon 2006; but see Lewis et al. 2002). At the Gannet Islands, murre and razorbills followed the same pattern; females had shorter foraging trip and fed the chicks more frequently (Paredes et al. 2006). The fact that sex differences only occurred during trips with meal delivery suggested that foraging tactics of males and females were motivated by their parental duties. Whether sex differences in trip duration were due to differential diving activity or distance to feeding areas was unknown.

The diving behaviour of murre has been extensively studied across their geographic range (Croll et al. 1992; Falk et al. 2000; Mehlum et al. 2001; Watanuki et al. 2001; Benvenuti et al. 2002; Mori et al. 2002; Jones et al. 2002; Watanuki et al. 2006). Only one study has examined possible differences between the sexes; they dived at different

times of day and duration underwater (Jones et al. 2002). The diving behaviour of razorbills has been studied much less and no studies have investigated possible sex differences (Benvenuti et al. 2001; Dall'Antonia et al. 2001; Watanuki et al. 2006). Sexes could potentially forage at different times because of differences in breeding site attendance patterns (i.e., murre: K. Woo in Gaston and Hipfner 2000; Jones et al. 2002; Paredes et al. 2006). In crested auklets (*Aethia cristatella* (Pallas, 1769)), males brood at night and dive by day, and they seem to be better suited to breeding-site defence and chick-guarding than females (Fraser et al. 2002). The male-biased capability in defending the chick, because of larger bill dimensions (see review by Gaston and Hipfner 2000) and more aggressive behaviour (R. Paredes and S. Insley, unpublished data), is one of the proposed explanations for partitioning of parental roles in murre and razorbills (Paredes et al. 2006). Thus, it is possible that foraging schedules were driven by the need of males to be at the breeding site at times when the chick is potentially in most danger. If this were true, we expect males in both species to show foraging schedules that correlate with their parental behaviour. Consequently, they could potentially forage under different at-sea environmental conditions than females (i.e., light levels or prey availability), and therefore affect their dive depth and prey taken (Wilson et al. 1993; Jones et al. 2002) differently. Physical (water depth) and ecological (prey species) constraints play major roles in the frequencies of dive types and other dive parameters in a multi-species comparison of seabirds and pinnipeds (Schreer et al. 2001).

Functional classification of dives based on dive shape (i.e., time–depth profile) has been done for several species of air-breathing animals (Kooyman et al. 1992; Schreer and Testa 1996; Schreer et al. 2001). U- and V-shaped dives are the most frequent types observed in murre (Croll et al. 1992; Elliott et al. 2008) and razorbills (Benvenuti et al. 2001; Dall'Antonia et al. 2001; Watanuki et al. 2006), respectively; however, whether sex differences occur is unknown. Using stomach-temperature recorders, some studies have been able to confirm associations between dive shape and feeding (Thompson et al. 1991; Wilson et al. 1992; Lesage et al. 1999). Thick-billed murre usually perform direct flights to the colony for chick delivery (Benvenuti et al. 2001). This distinctive behaviour has allowed for associations between dive shapes and specific prey species (Elliott et al. 2008). Others diving studies in northern gannets (*Morus bassanus* (L., 1758); Garthe et al. 2000) and king penguins (*Aptenodytes patagonicus* J.F. Miller, 1778; Pütz and Cherel 2005) have also reported relationships between prey species and dive profiles. Sex differences in prey delivered to chicks have been reported for razorbills at Skommer Island (Wagner 1997), which may reveal differences in dive profiles as well. Thus, the analysis of dive profiles in relation to prey and daytime may be useful for understanding the mechanisms behind sex differences in diving behaviour.

The aim of this study was to investigate (i) whether sexes of two sympatric sister-species, murre and razorbills, differ in their foraging behaviour and prey captured and (ii) whether these differences mirrored their parental roles. We specifically studied whether sexes differed in dive parameters, frequency of dives and dive bouts, dive type,

and prey species for chick-provisioning. Body mass and parental behaviour of a group of noninstrumented murres were investigated simultaneously to control for possible effects of attached gear on diving behaviour (Paredes et al. 2005).

## Methods

We conducted fieldwork during August 2000–2003 at one of the six Gannet Islands (GC4) located on the low Arctic coast of Labrador, Canada (53°56'N, 56°32'W). A mixed colony of about 150 pairs of murres and 45 pairs of razorbills were studied through the chick-rearing period. A total of 40 murres and 18 razorbills were captured for deploying time–depth recorders (TDRs). Fifteen additional razorbills were captured, as part of another ongoing study, for sex determination. Only one member of a pair was captured for TDR deployment while the other was brooding, so the chick (1–11 days old) was never left unattended. Murres were captured with a noose of nylon monofilament (1.5 mm diameter) on the end of a 4 m graphite pole. Razorbills were captured with a small weighted noose-carpet attached to one end of 20 m of nylon monofilament line (1.5 mm diameter) and with the other end attached to 3 m wooden pole. The noose-carpet was positioned on cliff ledges, so razorbills were captured by the leg as they approached or departed their breeding site. Two types of TDRs were deployed on murres: MK7 (Wildlife Computers, Redmond, Washington; 25 g, 3% of body mass, flat shape with pointed end) and LTD\_100s (Lotek Wireless Inc., St. John's, Newfoundland; 16 g, 2% of body mass, cylindrical shape with rounded end). Both TDRs are similar in size (5–8 cm × 1–2 cm × 1–2 cm) and in cross-sectional area (1.7–1.9 cm<sup>2</sup>, 1.2%–1.3% of the body area). We deployed LTD\_100 units on razorbills. TDRs were attached to back feathers using three strips of black TESA<sup>®</sup> tape, cable ties, and drops of cyanoacrylate glue ("Hot Stuff"<sup>®</sup>) under both ends of the device. Handling time from capture to release totalled 5–8 min. TDRs were programmed to sample depth every 5 s and depth resolution was 0.5 m. We recovered TDRs several days after deployment (murres: 1–4 days; razorbills: 2–7 days). Blood samples (0.5 mL) were taken from the tarsus vein and stored in vials with 95% ethanol for use in determining the bird's sex by DNA analysis (Fridolfsson and Ellegren 1999).

We performed daily observations of feeding of marked murres (15 pairs) and razorbills (31 pairs), including the instrumented birds, during most of the chick-rearing period. The observations were undertaken from a blind, using a spotting scope (20× to 60× magnification, 60 mm) and binoculars (10× magnification, 50 mm), from dawn to dusk (0400–2200). Prey delivered to chicks was recorded at the species level when possible. We identified individual birds by temporary marks of picric acid (yellow) or fluorescent paint (green, pink, and orange) delivered using a small container of the marking liquid attached to the tip of a 4 m pole. This allowed marking the birds from above without capturing them. The markings and key life-history information were recorded on identification cards for quick reference. One member of each pair was captured at the end of chick-rearing for permanent banding (a stainless steel and a

colour leg band) and sex determination. The sexing analysis was done after the season was finished, so the observers were blind to the sex of birds during behavioural data collection.

Data of ambient light intensity or total illumination (solar + lunar illumination) was inferred using astronomical ephemeris (available from <http://wise-obs.tau.ac.il/~eran/>). These calculations do not account for cloud coverage. Based on these records, we determined that twilight periods occurred around dawn from 0330 to 0530 and around dusk from 2000 to 2200.

## Data and statistical analysis

Dive data were analyzed using the dive analysis program from IKNOS toolbox (Y. Tremblay, unpublished data) developed with MATLAB software (The MathWorks, Natick, Massachusetts). The program was setup to analyze all dives equal to, or exceeding, 3 m depth (6 times depth resolution) and 15 s duration (3 times sampling interval). Dive parameters were calculated for each dive, following Tremblay and Cherel (2003). We determined maximum depth, duration, bottom time (the amount of time between 75% and 100% of the maximum depth reached), and descent and ascent rates for individual dives. We calculated diving efficiency as the proportion of the bottom time over a complete dive cycle (dive duration + postdive interval (PDI); Ydenberg and Clarke 1989). Because 95% of dives had a PDI < 2 times their mean dive duration, this threshold was chosen as a bout-ending criterion (Tremblay and Cherel 2003). Dive profiles were classified visually into five dive shape categories: V-, U-, square-, W-, and asymmetrical.

Of the 40 TDRs deployed on murres, 30 obtained data, 7 had anomalous data, and 3 fell off the birds before recapture. We were unable to compare data between the sexes from both types of TDRs (MK7: 11 males and 15 females; Lotek: 3 males and 1 female) directly because only 1 female murre had a Lotek unit. This occurred because we did not know the sex of birds at the time of deployment. Nevertheless, because most of the birds had MK7 units (26 of 30), we compared the dive records of them against those of both TDRs together (MK7 + Lotek). In this way, we indirectly accounted for possible effects of type of TDR, and if the results were not affected by pooling the data, we assumed that this would allow us to include the Lotek data in the analysis. Of the 18 TDRs deployed on razorbills (all Lotek), 9 obtained data recordings (6 females and 3 males), 1 had no data (female), and 8 were never recovered.

A total of 4716 dives and 1668 dives were recorded from murres and razorbills, respectively. We only used a total of dives performed during entire days (murres — females: 1721 dives; males: 1927 dives; razorbills — females: 1082 dives; males: 473 dives) to be able to investigate time-of-day effects in diving behaviour.

We used mixed-factor models for the analysis of bouts, dive parameters, and dive shapes. The fixed factor was sex, and individual was used as the random factor. In this way, we were able to include the effect of individual variation in the model. Statistical analysis was carried out using SPSS version 11.5 (SPSS Inc., Chicago, Illinois). If residuals were not normally distributed, we transformed the dependent variable using log or square-root transformation as appropriate

before the analysis and presented coefficient of variation (CV) instead of standard deviation (SD). We report 95% confidence intervals instead of estimates of statistical power to address the question of type II error (Hoenig and Heisey 2001). Chi-square tests with Yates's correction were used to compare proportions. Relationships between parameters were analyzed using Pearson correlations. Values were expressed as means  $\pm$  SD. All comparisons were two-tailed and differences were considered significant when  $P \leq 0.05$

## Results

### Noneffect of TDR type

The mean depth of individual dives was not affected by TDR type (MK7:  $25.9 \pm 20.8$  m; both TDRs:  $27.5 \pm 21.1$  m; mixed-factor model:  $F_{[1,53]} = 0.053$ ,  $P = 0.818$ ), but was significantly affected by sex ( $F_{[1,28,21]} = 19.21$ ,  $P = 0.0005$ ). On average, male murrets ( $33.6 \pm 21.4$  m) dived 59% deeper than females ( $19.8 \pm 18.0$  m). Lack of significant effect of TDR type on the main factor allowed us to compare males and females in our analysis.

### TDR effect on body mass

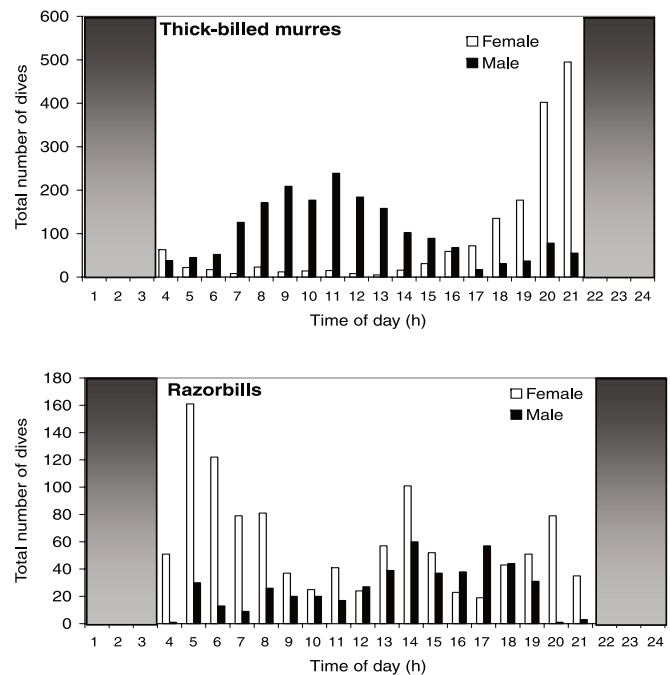
No sex differences were found in initial body mass in razorbills (female:  $701 \pm 51.8$  g,  $n = 14$ ; male:  $711 \pm 38.5$  g,  $n = 19$ ; Student's  $t$  test:  $t_{[1,31]} = -0.651$ ,  $P = 0.52$ ). On average, razorbills, regardless of sex (females:  $16.4 \pm 5.3$  g/day; males:  $13.7 \pm 3.5$  g/day; Student's  $t$  test:  $t_{[1,6]} = 1.040$ ,  $P = 0.338$ ) with TDRs lost  $15.0 \pm 4.8$  g/day during the deployment period. Male murrets had higher initial body mass and lost mass at higher daily rates than females (Paredes et al. 2005).

### Murre diving behaviour

Murrets at Gannet Islands showed a difference between the sexes in the time of day that foraging occurred (Fig. 1). Most female dives were between late afternoon and sunset (1800–2100, 70%,  $n = 1721$ ) and between early morning and after sunrise (0330–0600, 11%), while most male dives occurred during late morning to early afternoon (0800–1900, 67%,  $n = 1927$ ; Fig. 1). For twilight periods, females performed more dives near dusk (2000–2200, 56%) than dawn (0330–0530, 10%), while males performed only 7%–9% of their dives during these periods. Only 3% ( $n = 125$ ) of dives were recorded during darkness (2200–0300). These dives were shallow (<10 m) and were performed mostly by females (68%). Dive depth was positively correlated with inferred solar illumination; however, some deep diving (up to 102 m) was also performed at times (0500–0700) when total illumination was low (Fig. 2).

Male and female dive depths were affected differently by time of day (sex  $\times$  time:  $F_{[21,3574]} = 9.88$ ,  $P < 0.0005$ ; Fig. 2). The deepest dives of females occurred early in the morning (0500–0600; post hoc Tukey HSD test,  $P < 0.0001$ ) and, to a lesser degree, early in the afternoon (1500–1700; post hoc Tukey HSD test,  $P < 0.002$ ; Fig. 2). Deep diving by males also occurred early in the morning (0500–0700), but they occurred during mid-day and early afternoon as well (1200–1700; post hoc Tukey HSD tests,  $P < 0.01$ ). The dives of both males and females were significantly shallower immediately after sunrise (0300–0400) and

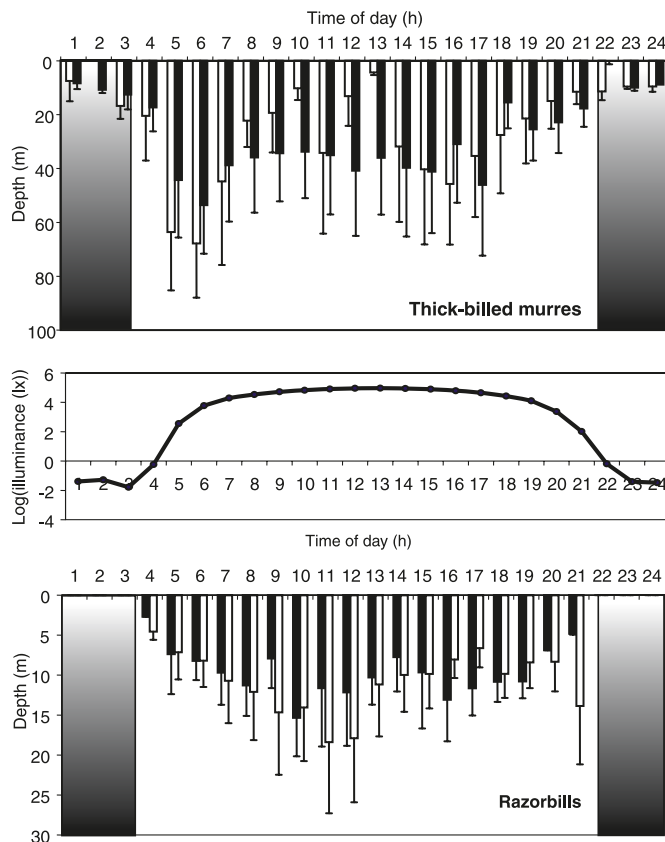
**Fig. 1.** Number of dives according to time of day of female (F) and male (M) thick-billed murrets, *Uria lomvia*, (16 F, 14 M) and razorbills, *Alca torda*, (6 F, 3 M) at Gannet Islands. Females dived more often at  $\leq 10$  and 19 m depths than males of razorbills and murrets, respectively ( $\chi^2$  tests:  $P < 0.0005$ ).



before sunset (2000–2300; post hoc Tukey HSD test,  $P < 0.001$ ; Fig. 2).

Most dives by females occurred at shallower depths, while most dives by males occurred deeper in the water column ( $\chi^2$  test:  $\chi^2_{[1]} = 562.43$ ,  $P < 0.0005$ ; Fig. 3). There were significant differences in the proportion of dive-shape groups between males and females ( $\chi^2_{[4]} = 385.46$ ,  $P < 0.0005$ ). On average, males dived significantly deeper (mixed-factor model:  $F_{[1,28]} = 20.015$ ,  $P < 0.0001$ ) and longer (mixed-factor model:  $F_{[1,28]} = 16.55$ ,  $P < 0.0005$ ) than females (Table 1). Females ( $n = 1721$ ) had significantly more W-shaped dives than males ( $n = 1927$ ), while males had more U-shaped dives than females ( $\chi^2_{[1]} = 370.77$ ,  $P < 0.0005$ ; Table 3). We did not find sex differences among the other three groups of dive shapes, V-shaped, square-shaped, and other asymmetrical shapes of males (3%) and females (3%;  $\chi^2_{[2]} = 4.91$ ,  $P = 0.086$ ; Table 3). On average, W-shaped dives ( $n = 2133$ ) were significantly shallower than U-shaped dives ( $n = 1144$ ; mixed-factor model:  $F_{[1,68,55]} = 89.84$ ,  $P < 0.0005$ ; Table 2). Females performed most W-shaped dives (70%) immediately before sunset (2000–2200) and most U-shaped dives during late afternoon onwards (67%, 1500–2000) and early morning (16%, 0400–0600). In contrast, W-shaped and U-shaped dives of males were distributed in a similar manner according to hour of day (0500–1600). During nighttime (2130–300) both sexes performed only W-shaped dives. These differences in the timing of diving between sexes correlated with differences in the parameters of dives of different shapes. W-shaped dives of males were significantly deeper (mixed-factor model:  $F_{[1,31]} = 15.648$ ,  $P < 0.0005$ ) and longer ( $F_{[1,31]} =$

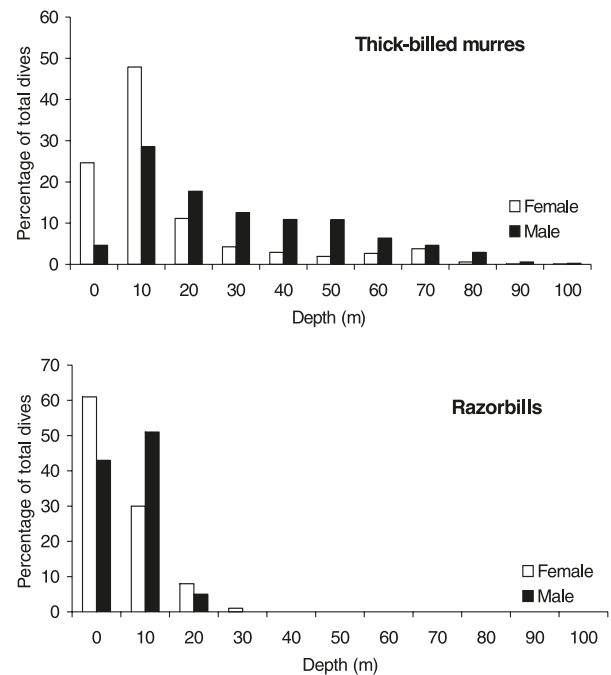
**Fig. 2.** Variation of dive depth of male (solid bars) and female (open bars) thick-billed murres (*Uria lomvia*) and razorbills (*Alca torda*) according to time of day (means + SD) and total illumination (solar and moon illumination) at Gannet Islands. Dive depth correlated with illumination in murres ( $r^2 = 0.389$ ,  $P < 0.0001$ ) and razorbills ( $r^2 = 0.236$ ,  $n = 1668$ ,  $P < 0.0001$ ). Sexes were affected differently by time of day (mixed-factor models: sex  $\times$  time,  $P < 0.0005$ ).



8.781,  $P = 0.006$ ) than those of females. Likewise, W-shaped dives of males had longer bottom time ( $F_{[1,31]} = 13.19$ ,  $P = 0.001$ ), faster ascent rate ( $F_{[1,31]} = 13.37$ ,  $P = 0.001$ ), and longer PDI ( $F_{[1,31]} = 9.57$ ,  $P = 0.004$ ) than those of females (Table 2). No sex differences were found in descent rate and dive efficiency of W-shaped dives ( $P > 0.05$ ; Table 2). We did not find differences in any diving parameters of U-shaped dives between males and females (mixed-factor models:  $P > 0.05$ ; Table 2).

Dive duration was positively correlated with depth (duration = 14.9 m/s depth + 0.4 s;  $r^2 = 0.89$ ,  $P = 0.001$ ) and PDI in murres (PDI = 24.4 s + 0.8 duration;  $r^2 = 0.65$ ,  $P < 0.001$ ). Dive depth affects other dive parameters in murres (Paredes 2008). Males dived deeper and had longer bottom time, PDI, dive cycle, and faster ascent and descent rates than females (mixed-factor models:  $P < 0.007$ ; Table 1). Despite differences in dive depth, sexes did not differ in diving efficiency (Table 1). Males had longer bouts than females (mixed-factor model:  $F_{[1,28]} = 7.66$ ,  $P = 0.009$ ), but they did not differ in the daily number of dives and bouts per day and in the number of dives per bout (mixed-factor models:  $P > 0.05$ ; Table 1).

**Fig. 3.** Frequency of dive depths (10 m depth interval) of female (F) and male (M) thick-billed murres, *Uria lomvia*, (16 F, 14 M) and razorbills, *Alca torda*, (6 F, 3 M) at Gannet Islands, Labrador.



#### Murre dive profiles in relation to prey type

Dives of murres were mostly W-shaped (59%) and U-shaped (31%), and to a lesser extent square-shaped (5%), V-shaped (3%), or other asymmetrical shapes (3%). The number of W-shaped and U-shaped dives varied according to dive depth in opposite directions. The proportion of W-shaped dives decreased with depth, whereas the proportion of U-shaped dives increased with depth (Fig. 4). Shallow W-shaped dives were significantly shorter in duration ( $F_{[1,6533]} = 69.26$ ,  $P < 0.0005$ ) and had slower descent rates ( $F_{[1,75.79]} = 24.65$ ,  $P < 0.0005$ ) than U-shaped dives. Log-PDI was significantly shorter in W-shaped dives than U-shaped dives (mixed-factor model:  $F_{[1,68.44]} = 39.42$ ,  $P < 0.0005$ ). Diving efficiency was significantly higher in W-shaped dives than U-shaped dives (mixed-factor model:  $F_{[1,64.41]} = 18.25$ ,  $P < 0.0005$ ). These differences in dive parameters between dive profiles may indicate specific methods of capture for various prey species of males and females.

Murres delivered to their young mainly daubed shanny (*Leptoclinus maculatus* (Fries, 1838); 83% by number,  $n = 956$ ), followed by capelin (*Mallotus villosus* (Müller 1776); 10%). All other prey species, such as sand lance (genus *Ammodytes* L., 1758), snake blennies (genus *Lumpenus* Reinhardt, 1836), eelpout (genus *Lycodes* Reinhardt, 1831), arctic cod (*Boreogadus saida* (Lepechin, 1774)), and invertebrates added up to only 7% of prey delivered to chicks. We observed three cases of crustaceans, which were delivered by females only at about 0500 in the morning.

Prey fed to chicks differed significantly between the sexes ( $\chi^2_{[2]} = 13.91$ ,  $P = 0.016$ ). Both sexes fed their chicks mainly daubed shanny (males: 82%,  $n = 441$  items; females: 84%,  $n = 515$  items); however, males provided significantly more

**Table 1.** Dive parameters of female (F) and male (M) thick-billed murres, *Uria lomvia*, (16 F, 14 M) and razorbills, *Alca torda*, (6 F, 3 M) at Gannet Islands, Labrador.

	Thick-billed murre		Razorbill	
	Female (mean ± SD)	Male (mean ± SD)	Female (mean ± SD)	Male (mean ± SD)
Dive depth <sup>a</sup> (m)	19.7±17.89	34.5±21.3*	9.94±5.78	10.4±4.94
Dive duration (s)	88.8±44.33	120.1±44.1*	48.3±14.7	52.1±11.7
Bottom time (s)	35.8±17.8	47.1±17.2**	19.2±5.22	21.8±5.94*
Ascend rate (m/s)	0.59±0.24	0.82±0.29*	0.61±0.25	0.65±0.26
Descend rate (m/s)	0.76±0.27	0.88±0.26*	0.54±0.18	0.54±0.17
Postdive interval <sup>b</sup> (s)	43.6±50.3	66.3±50.9*	25.1±22.8	25.1±23.1
Dive cycle <sup>b</sup> (s)	127.8±79.9	182±82.1*	74.9±29.2	78.1±16.4
Diving efficiency <sup>b</sup> (s)	0.33±0.13	0.31±0.12	0.32±0.09	0.33±0.10
No. of dives per day	53.7±25.2	49.4±29.9	54.1±26.4	43.0±34.7
No. of bouts per day	11.0±4.69	10.4±4.62	17.3±8.35	13.4±7.35
Dive-bout duration (s)	1296±334	1878±298**	825±323	1070±434*
No. of dives per bout	5.05±2.48	4.62±2.00	3.31±1.41	3.00±1.60

**Note:** \*,  $P \leq 0.009$ ; \*\*,  $P < 0.0005$ .

<sup>a</sup>Maximum depths — murres: females = 102 m, males = 110 m; razorbills: females = 36 m, males = 27 m.

<sup>b</sup>These excluded preceding dives to bout intervals in murres (females,  $n = 1318$ ; males,  $n = 1464$ ) and razorbills (females,  $n = 697$ ; males,  $n = 316$ ).

**Table 2.** Statistical comparisons of parameters of W-shaped and U-shaped dives between female and male thick-billed murres (*Uria lomvia*).

	U-shape			W-shape		
	Female (mean ± SD)	Male (mean ± SD)	Total (mean ± SD)	Female (mean ± SD)	Male (mean ± SD)	Total (mean ± SD)
Dive depth (m)	40.7±25.7	45.3±20.8	44.2±22.1**	13.4±7.67	21.5±11.8**	16.6±10.3
Dive duration (s)	136±61.2	138±44.6	138±49.3**	75.0±26.2	97.1±26.9*	87.8±28.6
Bottom time (s)	46.2±24.8	48.1±18.1	47.6±20.5	32.6±12.1	45.5±14.3*	37.7±14.6
Ascend rate (m/s)	0.74±0.25	0.89±0.27	0.85±0.27	0.55±0.21	0.76±0.29*	0.63±0.26
Descend rate (m/s)	0.91±0.28	0.99±0.21	0.97±0.23**	0.70±0.25	0.76±0.24	0.73±0.24
Postdive interval <sup>a,b</sup> (s)	56.6±4.64	66.5±3.19	64.1±3.55**	22.7±10.3	34.8±6.09*	26.9±8.62
Dive efficiency <sup>a</sup>	0.27±0.12	0.27±0.12	0.27±0.12	0.35±0.12	0.36±0.11	0.35±0.12**

**Note:** \*,  $P < 0.006$ ; \*\*,  $P < 0.0005$ .

<sup>a</sup>These excluded preceding dives to bout intervals (females,  $n = 1032$ ; males,  $n = 669$ ).

<sup>b</sup>Data was log-transformed before the analysis (CV instead of SD is shown in the table).

capelin than females (12% vs. 7%, respectively;  $\chi^2_{[1]} = 6.96$ ,  $P = 0.008$ ; Fig. 5).

We assumed that the prey item delivered to the chick was caught on the last dive. The last dives corresponding to daubed shanny delivery were mostly U-shaped (77%,  $n = 13$ ), while the rest were single dives of square-shaped, V-shaped, and asymmetrically shaped. Half of the last dives followed by capelin delivery ( $n = 4$ ) were U-shaped and half were square-shaped. No prey deliveries to chicks followed W-shaped dives.

### Razorbill diving behaviour




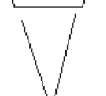
Razorbills dived deeper at times when total illumination was higher (Fig. 2). Male and female depth of dive was affected differently by time of day (sex  $\times$  time:  $F_{[1,1511]} = 9.183$ ,  $P < 0.0005$ ; Fig. 2). By analyzing the sexes independently, we found that the dives of females were significantly shallower at 0400 (post hoc Tukey HSD test:  $P < 0.003$ ) and deeper between 1100 and 1200 than other times of the day (post hoc Tukey HSD test:  $P < 0.008$ ). These times coin-

cided with lowest and highest illumination levels at Gannet Islands (Fig. 1). In contrast, the dive depths of male razorbills did not differ significantly among hours (post hoc Tukey HSD test:  $P > 0.05$ ). We excluded 3 h periods (0400, 2000, and 2100) in the post hoc analysis for males because of the small sample size.

Razorbills started and finished foraging at 0400 and 2200, respectively; very few dives were recorded after dark (Fig. 1). There was no clear division of foraging times between sexes; males and females foraged throughout the day. Nevertheless, about half of the dives of females were concentrated at morning hours (0400–0800), while 58% of the dives of males occurred at mid-day and early-afternoon hours (1300–1700; Fig. 1). At twilight periods, females performed more dives around dawn (0330–0530, 31%) than around dusk (2000–2200, 10%). Overall, males performed fewer dives around dawn (9%) and dusk (0.8%), respectively, than females.

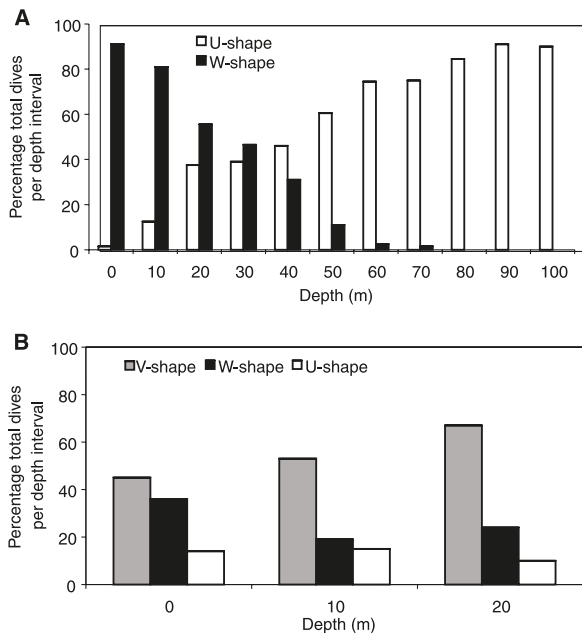
A multivariate mixed-factor analysis of the main razorbill dive parameters (depth, duration, ascent and descent rates,

**Table 3.** Frequencies of the main type of dives of thick-billed murres (*Uria lomvia*) and razorbills (*Alca torda*) at Gannet Islands, Labrador.

Dive shape	Razorbill		Thick-billed murre	
	Female (%)	Male (%)	Female (%)	Male (%)
	6	21*	17	45*
	38	18*	75	44*
	1	6*	4	6
	43	40	2	3

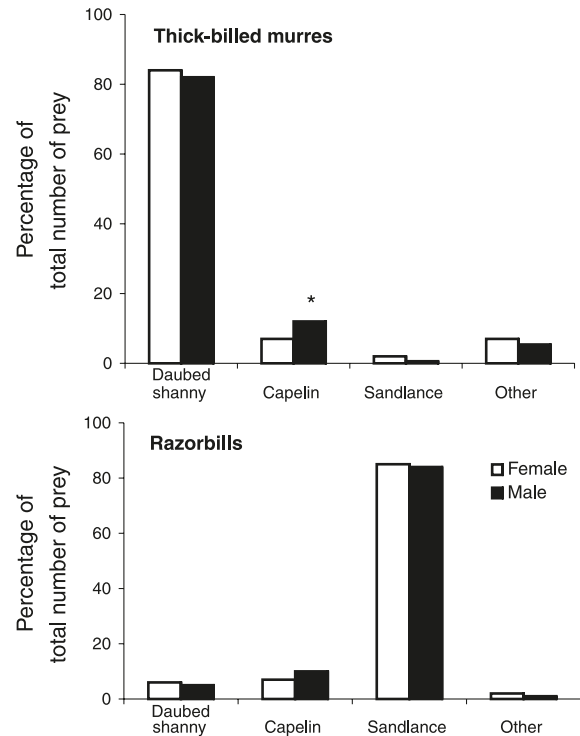
Note:  $\chi^2$  tests: \*,  $P < 0.0005$ .

**Fig. 4.** Sex differences in the frequency of the main dive-shape categories by depth: (A) thick-billed murres, *Uria lomvia*, (U- and W-shaped) and (B) razorbills, *Alca torda*, (V-, U-, and W-shaped). Proportions of dive shapes are based on the total number of dives per 10 m depth intervals.



and bottom time) indicated that diving behaviour differed by sex in razorbills (MANOVA: Wilks'  $\lambda = 0.948$ ,  $F_{[5,7]} = 12.46$ ,  $P < 0.005$ ). The univariate mixed-factor analysis of depth and other dive parameter showed no significant differences between sexes (mixed-factor models:  $P > 0.05$ ), except for bottom time (mixed-factor model:  $F_{[1,7]} = 8.224$ ,  $P = 0.020$ ). The mean dive depths of both sexes were within the 95% confidence limits of the grand mean of depth (9.78–10.43 m), although males were close to the upper bound limit. The mean values of males were above the upper bound of the 95% confidence limits of the grand

**Fig. 5.** Prey species delivered by female and male thick-billed murres (*Uria lomvia*) and razorbills (*Alca torda*) at Gannet Islands. Asterisk denotes statistical differences between the sexes ( $\chi^2$  test:  $P = 0.008$ ).



mean of dive duration (49.11–50.80 s) and ascent rates (0.60–0.62 m/s), which indicate a type II error.

Female razorbills performed more dives <10 m in depth, while males performed more dives >10 m ( $\chi^2_{[1]} = 60.933$ ,  $P < 0.0005$ , Fig. 3). There were significant differences in the distribution of dive types for males and females ( $\chi^2_{[4]} = 147.34$ ,  $P < 0.0005$ ). Males had significantly more U-shaped and square-shaped dives than females, and females had more W-shaped dives than males ( $\chi^2_{[2]} = 144.97$ ,  $P < 0.0005$ ; Table 3). No sex differences were found in the proportion of V-shaped dives or other asymmetrical dives ( $\chi^2_{[1]} = 2.27$ ,  $P = 0.14$ ). V-shaped dives ( $11.9 \pm 5.9$  m) were significantly deeper than W-shaped ( $8.8 \pm 5.4$  m) and U-shaped dives ( $9.6 \pm 4.4$  m; mixed-factor model:  $F_{[2,28.7]} = 4.08$ ,  $P = 0.028$ ) in razorbills. No differences in dive depth were found between W-shaped and U-shaped dives (post hoc Tukey HSD test:  $P = 0.20$ ).

Between sexes, no differences were found in any dive parameter of the three dive categories (mixed-factor models,  $P > 0.05$ ), except for bottom time. V-shaped dives ( $19.2 \pm 4.4$  s) and W-shaped dives ( $22.9 \pm 5.7$  s) of male razorbills had longer bottom times than those of female razorbills (V-shaped,  $17.7 \pm 3.6$  s; mixed-factor model:  $F_{[1,8.41]} = 8.34$ ,  $P = 0.02$ ; W-shaped,  $20.2 \pm 5.9$  s;  $F_{[2,16.64]} = 5.07$ ,  $P = 0.004$ ).

Dive duration correlated with depth (duration = 4.15 m/s depth + 0.29 s;  $r^2 = 0.74$ ,  $P = 0.001$ ) and PDI (PDI = 8.786 s + 0.31 duration;  $r^2 = 0.19$ ,  $P < 0.001$ ) in males and females. Despite slight differences in depth between the sexes, there were no intersexual differences in PDI, dive

cycle, and diving efficiency (mixed-factor models:  $P > 0.05$ ; Table 1). The mean values of both sexes were within the 95% confidence limits of the grand means for each variable. Males had longer bouts than females (mixed-factor model:  $F_{[1,7]} = 8.416$ ,  $P = 0.023$ ), but they did not differ in the daily number of dives or bouts and the number of dives per bout (mixed-factor models:  $P > 0.05$ ; Table 1). The mean values of the sexes were within the 95% confidence interval limits of the grand means of bouts per day, dives per day, and dives per bout.

### Razorbill dive profiles in relation to prey type

Most dive profiles of razorbills were V-shaped (42%) and W-shaped (32%), and to a lesser extent U-shaped (11%), square-shaped (2%), and other asymmetrical shapes (14%). The proportion of V-shaped dives increased with depth and the proportion of W-shaped dives tended to decrease with depth (Fig. 4). The proportion of U-shaped dives did not vary with dive depth in razorbills (Fig. 4). Dive duration did not differ between the three dive categories (V-shaped,  $51.9 \pm 14.9$  s; W-shaped,  $47.7 \pm 14.6$  s; U-shaped,  $50.8 \pm 9.3$  s; mixed-factor model:  $F_{[2,31.1]} = 0.96$ ,  $P = 0.39$ ). U-shaped dives ( $25 \pm 5.5$  s) and W-shaped dives ( $20.7 \pm 5.0$  s) had significantly more bottom time than V-shaped dives ( $18.2 \pm 3.9$  s; mixed-factor model:  $F_{[2,40.95]} = 16.53$ ,  $P < 0.0001$ ). Bottom times of U-shaped dives were significantly longer than W-shaped dives (post hoc Tukey HSD test:  $P < 0.0001$ ). No differences were found among the three dive shapes in other dive parameters or PDI (mixed-factor models,  $P > 0.05$ ). Dive efficiency was significantly higher in U-shaped dives (0.38, CV = 1.14%) than W-shaped (0.34, CV = 2%) and V-shaped dives (0.27, CV = 3.3%; square-root transformation and mixed-factor model:  $F_{[2,32.41]} = 12.56$ ,  $P < 0.0001$ ). W-shaped dives were significantly more efficient than V-shaped dives (post hoc Tukey HSD test:  $P < 0.0001$ ).

Razorbills delivered mainly sand lance (85% by number,  $n = 1685$ ) and less frequently capelin (8%), daubed shanny (6%), and "other" species (1%) such as blennies (*Lumpenus* sp.), eelpout, Atlantic cod (*Gadus morhua* L., 1758), and crustaceans. The composition of prey species delivered to chicks at the breeding site did not differ between male and female razorbill parents ( $\chi^2_{[3]} = 6.69$ ,  $P = 0.08$ ). Both sexes fed their chicks primarily sand lance (females: 85%,  $n = 884$ ; males: 84%,  $n = 548$ ), and although males delivered more capelin (10%) than females (7%), this difference was not statistically significant ( $\chi^2_{[1]} = 3.48$ ,  $P = 0.07$ , Fig. 5).

## Discussion

### Effect of time–depth recorders on the behaviour of birds

The effect of experimentally attached gear on seabirds is a neglected subject, yet the effects may be significant. Murres equipped with TDRs were shown previously to experience a reduction in body mass, parental effort (provisioning and brooding), and foraging-trip duration (Paredes et al. 2005). In razorbills, no sex differences were found in initial body mass and daily rates of mass loss during the TDR deployment period. No data were available for the effect of instrumentation on parental and foraging behaviours

of razorbills. However, we assumed that both murres and razorbills were negatively affected by the extra work of carrying TDRs. These behaviours are likely to be due to a reduction in the diving and (or) flying performance of the birds, so we are aware that our measurements are likely underestimates or overestimates. Nevertheless, because male and female murres and razorbills are almost identical in mass and morphometrics, except for bill size (Gaston and Jones 1998), and were treated identically in our procedures, we assumed that sex differences in foraging behaviour would occur as a result of naturally different strategies and not because of the effect of attached devices. In fact, males and females of both species did not differ in the number of dives per bout and dives per day, and both were able to dive to similar maximum depths, which suggested no differential TDR effect on the sexes underwater.

### Patterns and differences in diving behaviour of sympatric murres and razorbills

At Gannet Islands, murres dived (up to 110 m) deeper than razorbills (up to 36 m) and characteristically performed U- and V-shaped dives, respectively, which concur with other studies (Croll et al. 1992; Benvenuti et al. 2001; Dall'Antonia et al. 2001; Watanuki et al. 2006). Furthermore, we found that W-shaped dives were also common in both murres (59%) and razorbills (32%). Occurrences of U-shaped dives increased with depth in murres; the same relationship has been reported in blue-footed boobies (*Sula nebouxii* Milne-Edwards, 1882; Zavalaga et al. 2007). The analysis of dive type in relation to prey species suggested that U-shaped dives in murres were used for capturing mid-bottom species like daubed shanny and capelin. Although the sample size of prey deliveries by TDR-equipped murres ( $n = 20$ ) was not large enough to yield conclusive results, other seabird studies support our findings. In murres, U-shaped dives preceded deliveries of daubed shanny (Elliott et al. 2008); in northern gannets, U-shaped dives preceded regurgitations of capelin (Garthe et al. 2000). The fact that sand lance was the main prey species delivered by both razorbill sexes, and that both sexes also had similar frequencies of V-shaped dives in this study, suggested that this dive type was a result of a specific method of capture underwater. Sand lance schools characteristically form a tight ball when attacked underwater (Hamilton 1971, Grover and Olla 1983), which can make the group more vulnerable to aerial predators near the surface (see review by Willson et al. 1999). Razorbills could use buoyancy (threshold limit: 20 m; Watanuki et al. 2006) to enhance acceleration in capturing prey on the way back to the surface as has been suggested for other alcids (Burger et al. 1993). This behaviour may allow for a faster return to the same feeding spot; razorbills usually have consecutive dives at similar depths within a bout (Dall'Antonia et al. 2001).

Occurrences of W-shaped dives decreased with depth in both murres (deep divers) and razorbills (shallow divers), which supports that the visual classification of dive profiles were not biased by the difference in maximum depth. In addition, the resolution of the diving program used for the classification allowed for distinguishing zig-zags (W-shaped dives) from small wiggles at different depths clearly. U- and W-shaped dives represent different prey-capturing strategies

in penguins, with prey pursuit occurring predominantly during the ascent and bottom phases, respectively (Kirkwood and Robertson 1997; Ropert-Coudert et al. 2000). Furthermore, predators should be able to spend longer time at the bottom of a dive when feeding on smaller prey (i.e., crustaceans) than on larger prey (i.e., fish) because of differences in swim speed (Wilson et al. 2002). We found that murre spent proportionately more time at the bottom of a complete W-shaped dive cycle than of a U-shaped dive cycle (diving efficiency). The same results have been reported for king penguins; W-shaped dives were more effective than U-shaped at twilight periods probably for capturing crustaceans (Pütz and Cherel 2005). Murre and, to a lesser extent, razorbill performed more W-shaped dives at twilight and night periods as well. Although we observed few cases of crustacean delivery to chicks (murre 0.3%, razorbill 0.4%), the consistent reddish coloration of the guano covering the ledges in the murre colony suggests that crustaceans are a main part of the adult diet there and at Coats Island (Croll et al. 1992). Crustaceans are also an important part of adult murre and razorbill diets, especially in the winter (Mehlum et al. 1996; Mehlum 2001; Hipfner and Chapdelaine 2002; see also Rowe et al. 2000). The analysis of the last dive in relation to prey delivered to chicks showed that W-shaped dives never preceded chick-feeding, suggesting that they were used mostly for self-feeding at Gannet Islands.

#### **Sex differences in diving behaviour and intersexual patterns in murre and razorbill**

Diving behaviour of murre did not closely track the diurnal pattern of light intensity. Although both sexes dived shallower at twilight, they dived deeper at different times of day (e.g., females at sunrise) regardless of light levels. Deep diving coincided with peaks of chick-provisioning for each sex (Paredes et al. 2006), which likely targeted daubed shanny (benthic fish, Bryant and Jones 1999; this study). Incubating murre feeding entirely for self-feeding dived shallower than chick-rearing birds at Hakluyt (77°26'N; Benvenuti et al. 2002), which suggests that differences exist in foraging for provisioning and self-feeding. In razorbill, dive depth varied with light intensity, being deeper at midday and shallower around dawn and dusk. Diving was infrequent at night. However, this pattern was mainly observed in female razorbill, which seem to track the diurnal patterns of sand lance. This shallow prey species is light sensitive and stays under the sand during the night and emerges and roams in the water column during daytime (Winslade 1974; Hobson 1986; Ostrand and Gotthardt 2005). Male razorbill did not differ in dive depth throughout the day (except twilight) and tended to deliver more secondary prey species than females. Both male murre and razorbill appeared to deliver more capelin and performed significantly more U-shaped dives than females. Capelin is a pelagic fish that moves in schools at variable depths of the water column (Montevecchi and Piatt 1984; Davoren et al. 2006) and typically follows the vertical migration of zooplankton at night (see review Mowbray 2002). During the breeding season of auks, mature capelin are found at sites near shore (<50 m depth), probably owing to spawning behaviour, while other age classes were found at intermediate (50–100 m) and

deeper (up to 250 m) depths off Newfoundland (Davoren et al. 2006). Stable isotope analysis suggested that breeding razorbill have a stronger tendency to feed in nearshore waters than murre (Thompson et al. 1999). Thus, male razorbill were likely feeding on spawning shoals of capelin at depths up to 30 m, while male murre were likely foraging on deeper shoals of capelin offshore. Although razorbill usually dive in shallow waters (reviewed by Hipfner and Chapdelaine 2002; this study), they can dive as deep as 140 m (Jury 1986), suggesting that light intensity may not be a limitation for this species. Altogether, these results suggest that diving behaviour in razorbill and murre was determined by the behaviour of their prey, which may largely depend on times and places each sex foraged for either provisioning or self-feeding.

Sex differences in dive parameters and timing of diving behaviour were found in both murre and razorbill at Gannet Islands, although a less clear division between the sexes occurred in razorbill (consistent with other studies; Wanless and Harris 1986; Wagner 1992). Among murre, the sex difference in dive depth could be attributed to the consistent differences in breeding-site attendance and foraging schedules of each sex (Jones et al. 2002; this study). The differences in other dive parameters such as dive duration, ascent and descent rates, bottom time, and PDI were a result of difference in maximum dive depths (Paredes 2008). In razorbill, the multivariate approach that combined the main dive parameters (depth, duration, bottom time, ascent rate, and descent rate) suggested that diving behaviour depended on sex. However, we did not find significant differences in mean depths and other dive parameters, except for bottom time, between the sexes using the univariate approach. The lack of significant differences between sexes in most of the dive parameters was probably due to the small sample size of male razorbill ( $n = 3$ ; type II error). Male mean values of depth, duration, and ascent rate were above the upper bound of the 95% confidence limits of the grand means. These results suggest a tendency for males to dive to deeper levels than females. In fact, we found that female razorbill tend to forage at twilight periods (mainly sunrise) and dive to shallower depths more often than males (61% vs. 42% of total dives) as occurs with female murre. The fact that female razorbill had shorter bout duration than males, despite similar number of dives per bout, supports their more frequent shallow diving. Thus, it seems that female murre, and to a lesser extent female razorbill, take advantage of the vertical migration of crustaceans to shallow depths during twilight periods at Gannet Islands. Consistent with these results, we found that both female murre and razorbill performed significantly more W-shaped dives than males. In addition, female murre had shallower W-shaped dives than males. This distinctive foraging behaviour may allow for faster self-feeding rates and consequently a more efficient provisioning in females (R. Paredes, unpublished data).

Sex differences in foraging-trip duration found in murre and razorbill at Gannet Islands (Paredes et al. 2006) may be partially accounted for by differences in diving activity. Dive duration and PDI decreased with depth in both species, which implied that females should have shorter dive cycles (dive duration + PDI) if they dive shallower than males. This explains how the sexes performed similar numbers of

dives per bout, but females had shorter bouts than males. Thus, although sexes had similar numbers of dives and bouts per day, females seemed to spend less time underwater than males, which may partially explain the differences in trip duration.

### Do parental roles determine foraging patterns and consequently diving behaviour?

We hypothesized that sex differences in diving behaviour could result from differences in foraging schedules determined by different parental roles of males and females at the Gannet Islands. As a result, sexes would forage under different at-sea environmental conditions (i.e., light levels or prey availability), which would in turn affect their dive depths and prey taken (Wilson et al. 1993; Jones et al. 2002) differently. The relatively similar intersexual segregation in feeding time and dive depth found in the two sympatric alcid species suggest that the observed foraging patterns were linked to the patterns of parental roles found at the Gannet Islands. We proposed that foraging schedules were driven by the need of males to be at the breeding site at times of higher chick vulnerability because of the greater ability of males to protect the chick (Paredes et al. 2006; R. Paredes and S. Insley, unpublished data). In both species, males spend more nights with the chick than females (Paredes et al. 2006), suggesting that males were present at the breeding site during twilight periods. Our results confirmed that females were more often diving at twilight periods (mainly sunrise in razorbills) and therefore males were present at the breeding site. Higher predation of chicks and kleptoparasitism rates occur at times when seabirds return from feeding sites, which coincides with sunrise and sometimes sunset (Oro and Martinez-Vilalta 1994; St. Clair et al. 2001; Williams and Ward 2006). These behaviours may potentially increase chick vulnerability to predation or dislocation during aggressive encounters between conspecifics and heterospecifics. One of the most distinctive life-history characteristics of the Alcini species is that the male is the caregiver that accompanies the chick to sea (Gaston and Jones 1998). Chick survival at departure, which mostly occurs at sunset, is a major constraint for these species (Gilchrist and Gaston 1997b). Males seem to be morphologically and behaviourally more capable of chick or egg defence because they have larger bills that can be used as weaponry and because they are more aggressive than females (R. Paredes and S. Insley, unpublished data.). Murres that defended eggs were able to reduce predation by glaucous gulls (*Larus hyperboreus* Gunnerus, 1767) compared with birds that did not (Gilchrist and Gaston 1997a). Thus, male presence at the breeding site at times when a chick is most at danger (i.e., sunrise and sunset) would potentially benefit the fitness of parents, and consequently determine foraging schedules.

The fact that different nest-attendance schedules, i.e., males diving at night and brooding during the day, have been reported for murres at Coat Islands (K. Woo in Gaston and Hipfner 2000) may be explained by differences in daylight periods and colony size. Larger bird colonies have greater nest competition and per-capita fight rates than smaller colonies because either nonbreeding floaters contest sites more persistently or more floaters visit larger colonies

(Brown and Brown 1996; Davis and Brown 1999). If breeding-site competition is a major constraint for larger murre colonies at Coat Island, then male presence through longer daylight periods (3 h more than at Gannet Islands) may be necessary to defend the breeding site and chicks against prospecting nonbreeders. Comparative studies between localities with different environmental conditions (i.e., light availability) and similar productivity are needed to confirm two major and related questions: (1) are the patterns of parental roles found at Gannet Islands general to these alcid species and (2) are these roles driven by the foraging behaviour of males and females during reproduction?

In conclusion, we found a similar temporal segregation of the sexes in dive foraging time, dive depth, and prey type during reproduction in two slightly dimorphic, sympatric, and closely related auks. Females dived at twilight periods and to shallower depths, on average, than males and this was reflected in their dive profiles. We propose that the different foraging schedules, and consequently dive depths, were driven by the need for males to be at the breeding site at times of higher chick vulnerability because of their better capability of defending the offspring.

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