

The influence of buoyancy and drag on the dive behaviour of an Arctic seabird, the Thick-billed Murre

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Abstract: We used time–depth recorders to investigate the behaviour of free-ranging Thick-billed Murres (*Uria lomvia* L., 1758) after attaching positively ($n = 9$), negatively ($n = 10$), or neutrally ($n = 9$) buoyant handicaps and increasing cross-sectional area by 3% (2.8 cm²; $n = 8$) or 6% (5.6 cm²; $n = 6$). When buoyancy was altered or drag increased, murres reduced dive depth and duration, suggesting that murres do not manipulate dive depth to obtain neutral buoyancy during the bottom phase. Ascent rate increased as the bird surfaced and mean ascent rate increased for deeper dives, presumably reflecting steeper dive angles and greater buoyancy during deep dives. For short dives (<150 s), preceding surface pauses were better correlated with dive depth and duration than succeeding surface pauses (surface pauses were “anticipatory”), suggesting that murres control inhalation rates based on anticipated dive depth and duration. Murres reduced ascent rate near the surface, possibly to reduce the risk of decompression sickness. Neutrally buoyant recorders attached to the legs had no effect on chick feeding frequencies or adult mass loss, suggesting that this attachment method may have the least effect on the foraging behaviour of alcids.

Résumé : Nous avons utilisé des enregistreurs des profondeurs en fonction du temps afin d'étudier le comportement des guillemots de Brünnich (*Uria lomvia* L., 1758) libres en nature, après leur avoir attaché des surcharges de flottabilité positive ($n = 9$), négative ($n = 10$) ou neutre ($n = 9$) ou avoir augmenté leur section transversale de 3% (2,8 cm²; $n = 8$) ou de 6% (5,6 cm²; $n = 6$). Lorsque la flottabilité est modifiée ou la traînée augmentée, les guillemots réduisent la profondeur et la durée de leurs plongées, ce qui indique qu'ils n'ajustent pas la profondeur de leur plongée afin d'obtenir une flottabilité neutre durant la phase profonde. Le taux de remontée augmente à mesure que l'oiseau s'approche de la surface et le taux de remontée moyen augmente lors des plongées plus profondes, ce qui est probablement le résultat d'angles de plongée plus prononcés et d'une flottabilité accrue lors des plongées profondes. Dans le cas des plongées courtes (<150 s), il y a une meilleure corrélation entre la profondeur de la plongée et la pause en surface qui la précède qu'avec la pause en surface qui la suit (les pauses en surface sont « anticipatrices »), ce qui indique que les guillemots contrôlent leur taux d'inhalation en fonction de la profondeur et de la durée anticipées de la plongée. Les guillemots réduisent leur taux de remontée près de la surface, peut-être pour réduire le risque de maladie des caissons due à la décompression. Des enregistreurs à flottabilité neutre attachés aux pattes sont sans effet sur les fréquences d'alimentation des petits, ni sur la perte de masse des adultes, ce qui porte à croire que cette méthode de fixation peut avoir un minimum d'effets sur le comportement de recherche de nourriture chez les alcidés.

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Introduction

Buoyancy and drag underpin the biomechanics of marine endotherms during diving. Buoyancy is the primary factor influencing diving behaviour in some species (Graham et al. 1987; Webb et al. 1998; Skrovan et al. 1999; Beck et al. 2000; Williams et al. 2000; Nowacek et al. 2001; Sato et al. 2002; Wilson et al. 2003; Hansen and Ricklefs 2004; Miller et al. 2004; Ropert-Coudert et al. 2004; Watanabe et al.

2006) and drag is the primary factor in others (Williams and Kooyman 1985; Williams et al. 1993; Lovvorn et al. 2004). The influence of buoyancy on cost of diving varies dramatically with dive depth in birds because air volumes in the respiratory system and plumage change with hydrostatic pressure (Wilson et al. 1992; Lovvorn et al. 1999, 2004; Gaston 2004; Enstipp et al. 2006). Penguins, cormorants, sea turtles, and whales may manipulate their air volumes or dive depths to optimize the effects of buoyancy on dive costs (Hustler 1992; Minamikawa et al. 2000; Sato et al. 2002; Wilson et al. 2003; Hays et al. 2004; Miller et al. 2004). However, as the thickness of the insulative layer of air in bird plumage is compressed with increasing depth, heat flux across this layer is expected to increase (Wilson et al. 1992; Grémillet et al. 1998), perhaps creating a conflict between decreased work against buoyancy and increased costs of thermoregulation. The influence of drag on dive costs, meanwhile, varies dramatically with swim speed, driving a trade-off between swim speed and energy expenditure (Lovvorn et al. 2004; Tremblay et al. 2005; Heath et al.

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2006). An increased layer of insulation may also result in increased cross-sectional area, which may increase drag, volume relative to mass, and buoyancy (Hansen and Ricklefs 2004).

Although drag and buoyancy both clearly influence the biomechanics of swimming in endotherms, precisely how these variables affect locomotion is still poorly understood. For example, buoyancy calculations depend heavily on estimates of the volume of air trapped within the feathers and respiratory system during diving. Estimates derived from dead or restrained individuals may not reflect volumes actually experienced during normal diving behaviour (Sato et al. 2002). Estimates for drag have been derived from laboratory experiments on frozen birds (e.g., Lovvorn et al. 1999, 2004), which may not completely account for drag associated with wing motion (profile drag), apparatus effects, and behavioural tactics (e.g., selecting gaits that reduce flow separation or that induce attached turbulent boundary layers to reduce skin friction) used by living birds and other animals to reduce drag. Drag coefficients for birds flying in air are believed to be lower than those obtained on frozen specimens in the laboratory owing to reduced flow separation behind living birds (Pennycuik 1997; Rayner 1999, 2001; Park et al. 2001; Ward et al. 2001; Tobalske et al. 2003; Elliott et al. 2004). Conversely, in some marine mammals drag coefficients are higher during active swimming than when measured on gliding or frozen specimens (Williams and Kooyman 1985; Fish 1988, 1993).

A complete understanding of avian biomechanics is important to understanding seabird behaviour, as seabirds modulate foraging behaviour in response to energy costs and assessed prey abundance and distribution (Mehlum et al. 1996; Grémillet and Wilson 1999; Davoren et al. 2003a, 2003b; Shaffer 2004; Tremblay et al. 2005). Understanding avian biomechanics is also essential for understanding the effect of recording devices on seabird behaviour (Gessaman and Nagy 1988; Obrecht et al. 1988; Bannasch et al. 1994; Culik et al. 1994). For example, recording devices have been found to increase workload without disrupting parental performance (e.g., seals: Boyd et al. 1991; Harcourt et al. 1995; seabirds: Weimerskirch et al. 1995; Kato et al. 2000; Shaffer et al. 2003) but can extend foraging trips (penguins: Croll et al. 1991; Watanuki et al. 1992; Hull 1997; Ropert-Coudert et al. 2000; Taylor et al. 2001), reduce chick provisioning (murre: Wanless et al. 1988; Watanuki et al. 2001; Hamel et al. 2004; Paredes et al. 2004), and reduce swim speed (Ropert-Coudert et al. 2006).

Thick-billed Murres (*Uria lomvia* L.) have been the focus of many biomechanical studies because their large size (~1 kg) and robust disposition have facilitated the use of recording devices and thus the accumulation of a large amount of data on diving behaviour (Croll and McLaren 1993; Benvenuti et al. 1998, 2002; Falk et al. 2000; Mehlum et al. 2001; Jones et al. 2002; Mori et al. 2002; Watanuki et al. 2001, 2003; Gaston 2004). Lovvorn et al. (1999, 2004) modeled diving behaviour in this species and concluded that the point of neutral buoyancy occurs at a depth of about 71 m. They also found that the cost of drag greatly exceeds the cost of buoyancy except during shallow (<20 m) dives. At our study site (see below), average dive depth has been previously reported as 18 m (Croll et al. 1992), suggesting

that buoyancy may be significant at this location, even during the bottom phase of a dive. Videotapes of diving murre show air bubbles being released during surfacing (Truitt 1996; Fothergill 2001), suggesting the potential for some active control of air volumes. Furthermore, penguins actively control buoyancy by manipulating respiratory air volume (Sato et al. 2002; Wilson 2003; Wilson et al. 2003), suggesting that neutral buoyancy is achieved during the bottom phase over a wide range of dive depths.

We designed an experimental study to complement the theoretical, laboratory, and observational work on the biomechanics of murre by Wilson et al. (1992), Lovvorn et al. (1999, 2004), Watanuki et al. (2003, 2006), Gaston (2004), and others. Specifically, we tested the hypothesis that murre manipulate dive depths, ascent/descent rates, and (or) air stores to compensate for changes in buoyancy. We experimentally manipulated buoyancy and drag in free-living murre and monitored changes in behaviour using time-depth recorders (hereafter, TDRs).

Materials and methods

Experiments were carried out at the west colony on Coats Island (62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005) during 2005. Thick-billed Murres were caught with a noose pole and weighed during each capture period. All procedures were approved by the University of Manitoba Animal Care Committee under the guidelines of the Canadian Council on Animal Care (protocol No. F04-030). Handling time was always less than 15 min and usually less than 5 min. Past observations indicated variation in time of breeding and site quality, but not feeding rates, across the colony (Hipfner et al. 1997, 2006). Owing to this, we captured individuals at four different sites (Jb, Q, T, and Z) for the buoyancy experiment. This experiment was conducted on incubating adults or adults with chicks less than 5 d old. The drag experiment was conducted on adults with chicks less than 12 d old. Owing to the small number of young chicks remaining by August, only a single site (Z) was used for the drag experiment.

Murre do not use their legs for underwater propulsion. Therefore, Lotek LTD_1100 TDRs (Lotek Wireless Inc., St. John's, Newfoundland, Canada) were secured with duct tape to plastic bands that were attached to the legs of murre during all experiments. These cylindrical TDRs (mass = 4.5 g; diameter = 1 cm; length = 3.3 cm) were attached parallel to the leg with the rounded end facing toward the body and the pressure sensor facing toward the foot. TDRs were programmed to sample temperature and depth every 3 s and were calibrated by the company prior to the field season with an accuracy of ± 0.1 m. A scuba diving session to 30 m prior to the field season revealed a precision of ± 0.1 m for four of the TDRs. Nonetheless, drift of ± 1 m was evident in some cases, and error was also present through changes in velocity and acceleration (Bernoulli effect); thus, total absolute error was likely about ± 2 m. In a parallel study, we attached TDRs to individuals during three 24–48 h feeding watches and recorded all prey items brought back by TDR-equipped individuals and their mates (Gaston et al. 2003, 2005). Observations were made from a blind 2–10 m away (Gaston et al. 2003).

Study design

During the incubation and chick-rearing periods of 2005 (15 July – 16 August), we attached three types of handicaps to the legs of breeding adult murres designed to mimic variation in buoyancy relevant to commercially available TDRs. Attachment of handicaps to the legs, immediately posterior to and contiguous with the body trunk, reduced the confounding effects of drag, as they were attached well behind the breakpoint for flow separation and did not increase frontal cross-sectional area (Bannasch et al. 1994; Culik et al. 1994). This point is further supported by the lack of an effect of neutrally buoyant handicaps attached to the legs on measured variables (see Results). However, attachment of positively or negatively buoyant handicaps to the legs may have resulted in additional dive cost by changing leg posture or body moment of inertia or by causing a yawing motion. These effects may have been reduced during ascent and descent (which make up the entirety of the V-shaped dives common at our study site) because gravitational and buoyant force vectors would be roughly in line with body motion at these times. Each handicap was constructed from three cylindrical plastic capsules (length = 3.4 cm; diameter = 1.3 cm), each with a total volume of $15 \pm 1 \text{ cm}^3$. The negatively buoyant handicaps (mass = $22.5 \pm 0.9 \text{ g}$) were filled with lead shot and then sealed with a wooden cork, epoxy, and duct tape. The positively buoyant handicaps (mass = $7.5 \pm 0.2 \text{ g}$) were sealed with a wooden cork, epoxy, and duct tape. The neutrally buoyant handicaps were left unsealed and weighed $15.0 \pm 0.1 \text{ g}$ when filled with water. Thus, the total buoyant force exerted by these handicaps was $0.075 \pm 0.01 \text{ N}$ downwards (negatively buoyant), $0.00 \pm 0.01 \text{ N}$ (neutrally buoyant), and $0.075 \pm 0.01 \text{ N}$ upwards (positively buoyant). A buoyancy of 0.075 N is 1.5% of murre surface buoyancy (4.50 N; Lovvorn et al. 1999) or ~50% of total murre buoyancy at 60 m. Because the plastic capsules would compress little with depth, the buoyancy of the positively buoyant handicaps did not change appreciably with depth.

The buoyancy experiment was completed for 11 negatively buoyant, 10 neutrally buoyant, and 9 positively buoyant individuals. To control for individual variation and breeding status, we monitored (with a TDR) each individual for an additional 24–48 h prior to attachment of handicaps or after removal of handicaps. In all cases, the entire experiment occurred within a 96 h period. For three neutrally buoyant, five negatively buoyant, and three positively buoyant individuals, the handicaps were attached for the initial 24–48 h, whereas for the remainder the handicaps were attached for the second 24–48 h period. There was no difference ($P > 0.6$) in dive depth, duration, descent rate, or ascent rate for any treatment between experiments in which the handicaps were attached during the first 24 h period and those in which they were attached during the second 24 h period. We visually inspected all handicaps after use. Two positively buoyant handicaps showed signs of leakage and were removed from analysis.

During chick rearing (5–16 August), we attached neutrally buoyant blocks for 24–48 h with cross-sectional areas of 2.8 ($n = 8$) or 5.6 cm^2 ($n = 6$), representing approximately 3% and 6% of total body cross-sectional area, respectively. The handicaps were roughly equivalent in cross section and size

to TDRs used in previous studies (e.g., Croll et al. 1992; Benvenuti et al. 2002; Jones et al. 2002). Each block measured 6.9 cm long, 1.5 cm high, and 3.7 or 1.85 cm wide and weighed 38.3 or 19.2 g after 30 min of submersion in salt water. The handicaps were made of plywood and, with less than 2% of the wood appearing above water, were effectively neutrally buoyant after 30 min of submersion in salt water. Grooves 1.4 cm wide and 0.7 cm deep were cut to aid in securing the handicap to the bird. We attached the handicaps to the back feathers of selected murres using cable ties and duct tape. Every effort was made to attach the handicaps parallel to the back and posterior to the wings. Order of attachment (e.g., “control” versus “handicap” period) was randomized by flipping a coin.

Prior to the experiment, we tested negatively ($n = 2$) and neutrally ($n = 2$) buoyant plastic handicaps and 5.6 cm^2 ($n = 2$) wooden handicaps to make sure they did not cause abandonment; all initial tests were successful. However, tests with three birds given a third back-mounted wooden handicap (length = 6.9 cm; cross-sectional area = 11 cm^2 ; mass = 65 g) were less successful. One of these individuals returned quickly without a handicap, another was not seen for 3 d, and the last was never seen again. All three chicks of these individuals fledged and in all cases the handicaps were designed to fall off after a few days as the tape became wetted.

Data analyses

All statistical procedures were completed in STATISTICA® (StatSoft Inc.). Prior to using parametric statistics, we tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levine’s test). Means are presented \pm SE. We analysed only dives with maximum depth $>3 \text{ m}$. To minimize any bias associated with the diel light cycle, all dives between 2200 and 0400 were excluded (Croll et al. 1992). Because we had strong a priori expectations, we used one-tailed paired t tests to compare dive depths and durations with and without handicaps. To compare ascent and descent rates, we included only dives $>20 \text{ m}$. We binned all dives in 10 m increments according to their maximum depth (e.g., 60–70 m, 70–80 m, etc.; see Fig. 1). For each TDR measurement, we calculated ascent and descent rates at a given sampled depth using the formula

$$U_n = \frac{\frac{d_{n+1}-d_n}{3} + \frac{d_n-d_{n-1}}{3}}{2} = \frac{d_{n+1} - d_{n-1}}{6}$$

where d_{n-1} , d_n , and d_{n+1} are the depths at consecutive 3 s sampling intervals and U_n is the vertical speed at sample time n . We examined ascent and descent rates only at depths more than 10 m above a given bin (e.g., for dive depths between 30 and 40 m, we examined ascent and descent rates only at depths above 20 m) to avoid including bottom time in our calculations for ascent and descent rates. We used one-tailed paired t tests to compare ascent and descent rates for each 10 m bin of depth. We included measurements only when we had data for at least five individuals for any given maximum depth. To eliminate the possibility that differences in dive depths were due to handicapped individuals reducing or increasing the proportion of non-feeding dives, we completed another set of analyses with dives $<20 \text{ m}$ excluded, as murres often do not forage during shallow dives (Croll et al. 1992). Because analyses

Table 1. Mean \pm SE decrease in dive depth, duration, ascent rate, and descent rate between handi-capped and non-handicapped Thick-billed Murres (*Uria lomvia*) at Coats Island, Nunavut, Canada.

Handicap	Depth (m)	Duration (s)	Ascent rate (m·s ⁻¹)	Descent rate (m·s ⁻¹)
B+ (<i>n</i> = 10)	19 \pm 9*	26 \pm 11*	0.06 \pm 0.05	0.12 \pm 0.06*
B- (<i>n</i> = 11)	7.9 \pm 3.0*	21 \pm 7*	0.13 \pm 0.05*	0.17 \pm 0.05 [†]
B0 (<i>n</i> = 9)	4.4 \pm 8.8	-0.6 \pm 12.0	0.06 \pm 0.05	0.01 \pm 0.02
2.8 cm ² (<i>n</i> = 8)	12 \pm 5*	9.1 \pm 6.8	0.13 \pm 0.06*	0.13 \pm 0.05*
5.6 cm ² (<i>n</i> = 6)	27 \pm 11*	46 \pm 14*	0.16 \pm 0.04 [†]	0.32 \pm 0.02 [†]

Note: B+, increased buoyancy; B-, decreased buoyancy; B0, neutral buoyancy; 2.8 cm², 2.8 cm² cross section neutral buoyancy; 5.6 cm², 5.6 cm² cross section neutral buoyancy. * and [†] denote significant differences from non-handicapped murres at $P < 0.05$ and $P < 0.01$, respectively (paired *t* test).

with dives <20 m excluded did not change the significance of any of our results, we discounted the possibility that the handicaps affected time spent participating in non-feeding dives. Consequently, we report only analyses with dives to all depths (>3 m) included. During descent, descent rates are “almost identical” to swim speeds (Lovvorn et al. 2004). We defined dive bouts for non-handicapped birds using sequential differences (Mori et al. 2001). A new bout was defined whenever the difference between sequential surface pauses exceeded 67 s or the difference between sequential depths exceeded 38 m (Mori et al. 2001). Within dive bouts, we examined the relationship between dive duration or depth and the duration of both the surface pause succeeding each dive and the surface pause preceding each dive. We classified dives <150 s as “short” and those >150 s as “long” based on a behavioural aerobic dive limit of 150 s (Croll et al. 1992) because we were interested in examining whether surface pauses preceding short dives were associated with air stores and whether surface pauses succeeding long dives were associated with lactate metabolism. To avoid issues with pseudoreplication, we completed analyses on surface pause and dive durations averaged over each individual (“individual murre basis”) as well as for all dives pooled (“individual dive basis”).

Results

Non-handicapped murres showed no change in mass during incubation ($t = -0.82$, $df = 21$, $P = 0.21$) or chick rearing ($t = -1.32$, $df = 51$, $P = 0.10$). Handicapped individuals declined in mass (negative buoyancy: mass loss = 36 \pm 11 g, $t = -3.27$, $df = 8$, $P = 0.006$; neutral buoyancy: 23 \pm 7.6 g, $t = -3.02$, $df = 9$, $P = 0.007$; positive buoyancy: 52 \pm 24 g, $t = -2.19$, $df = 6$, $P = 0.04$; 2.8 cm² drag: 36 \pm 11 g, $t = -3.22$, $df = 6$, $P = 0.009$; 5.6 cm² drag: 69 \pm 10 g, $t = -6.80$, $df = 5$, $P = 0.001$). Birds with TDRs showed no significant difference in frequency of chick feeding compared with their mates (TDR birds: 6.16 \pm 3.40 feeds per day; mates: 5.04 \pm 4.00 feeds per day; paired $t = 0.58$, $df = 24$, $P = 0.72$) or compared with themselves at an earlier or later date (TDR birds: 3.93 \pm 2.29 feeds per day; no-TDR birds: 3.12 \pm 2.64 feeds per day; paired $t = 1.85$, $df = 24$, $P = 0.96$).

Four out of 14 individuals with 2.8 cm² handicaps were never seen again, and the handicaps were therefore not removed and the data were not downloaded from the TDRs. In one case the chick appeared to have fledged prematurely (but apparently successfully) with the adult wearing the handicap. In another case the chick was depredated and the

adult reappeared at the colony on only one occasion. In the other two cases the handicapped individual appeared to have abandoned its chick, and the chick died after 36–60 h of intermittent care by the remaining parent. The 5.6 cm² handicaps never caused abandonment during 13 attachments (including three without TDRs, two that fell off before 24 h, and one for which no control period was obtained owing to problems with recapture).

Murres dove shallower, for shorter duration, and descended slower whenever drag or buoyancy was altered, but they showed no difference in these dive variables when neutrally buoyant handicaps were attached to the leg (Table 1). Murres ascended slower when buoyancy was decreased or drag increased, but they did not alter ascent rate when neutrally or positively buoyant handicaps were attached to the leg (Table 1).

Descent rates increased with depth to about 70–100 m ($F_{[20,241]} = 12.54$, $P < 0.001$; Fig. 1) but were independent of maximum dive depth ($F_{[30,247]} = 0.49$, $P = 0.97$). Ascent rates during a given dive were generally uniform between 80 and 140 m depth and then increased steeply at shallower depths (Fig. 1). Ascent rates also increased with maximum depth.

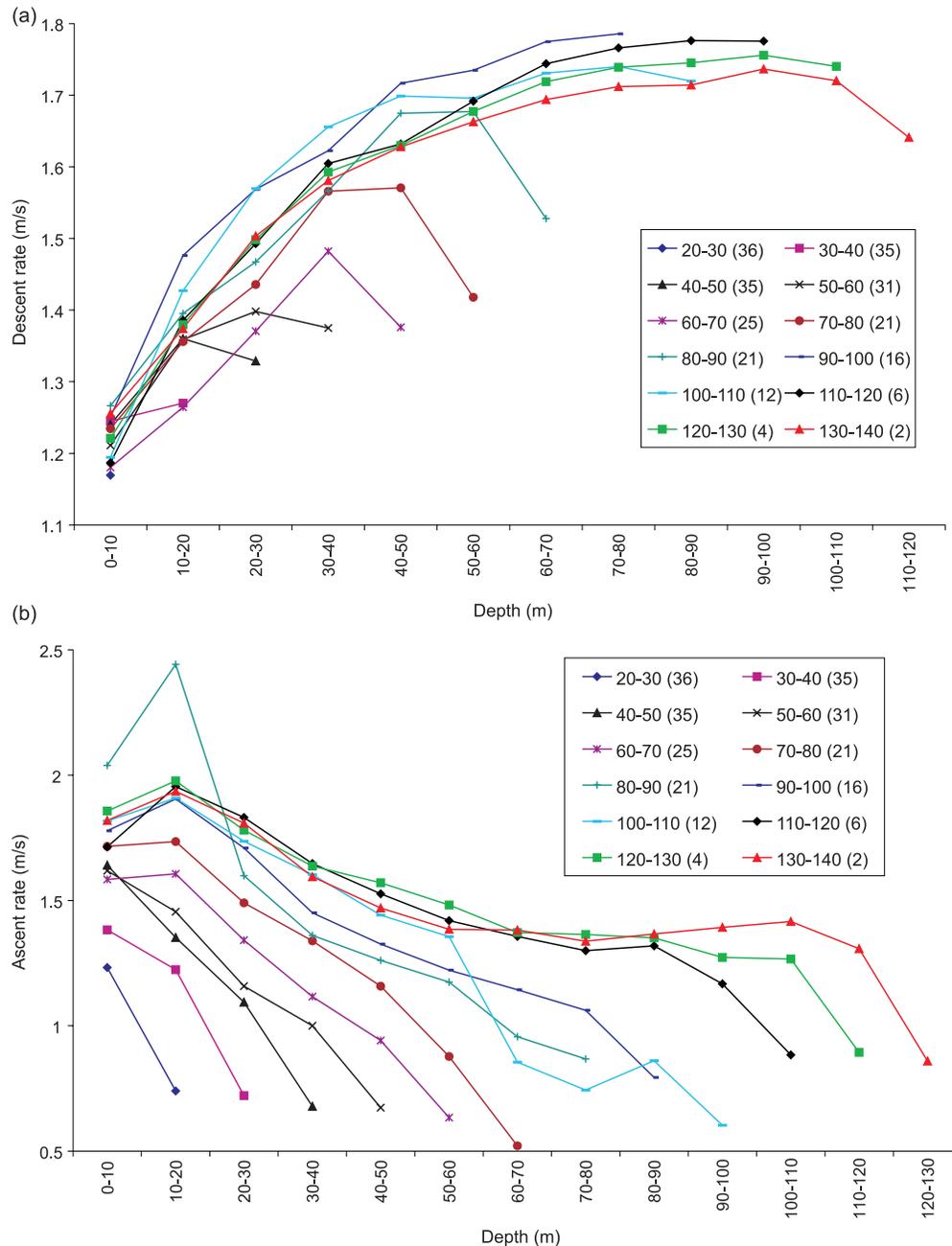
Overall, succeeding surface pauses (individual dive basis: $R^2 = 0.49$; individual murre basis: $R^2 = 0.90$) correlated just as well as preceding surface pauses ($R^2 = 0.50$ and 0.90) with dive duration. Succeeding surface pauses (individual dive basis: $R^2 = 0.56$; individual murre basis: $R^2 = 0.90$) also correlated just as well as preceding surface pauses ($R^2 = 0.56$ and 0.90) with dive depth. For long dives, surface pauses were reactive to dive duration (individual dive basis: $R^2 = 0.46$ vs. 0.41; individual murre basis: $R^2 = 0.73$ vs. 0.66), whereas for short dives, surface pauses were anticipatory to dive duration (individual dive basis: $R^2 = 0.33$ vs. 0.27; individual murre basis: $R^2 = 0.73$ vs. 0.66). Similarly, for long dives, surface pauses were reactive to dive depth (individual dive basis: $R^2 = 0.48$ vs. 0.42; individual murre basis: $R^2 = 0.78$ vs. 0.71), whereas for short dives, surface pauses were anticipatory to dive depth (individual dive basis: $R^2 = 0.34$ vs. 0.27; individual murre basis: $R^2 = 0.79$ vs. 0.70).

Discussion

Ascent and descent rates and buoyancy regulation

When buoyancy was altered or drag increased, murres reduced both dive depth and duration. This suggests that murres do not manipulate dive depth solely to obtain neutral buoyancy. Rather, murres likely choose dive depths depend-

Fig. 1. (a) Descent rates (m/s) relative to dive depth for dives with different maximum depths. (b) Ascent rates (m/s) relative to dive depth for dives with different maximum depths. Symbols denote mean values for non-handicapped Thick-billed Murres (*Uria lomvia*) diving to different maximum dive depths within each 10 m bin (number of individuals in parentheses).



ing on expected energy gain relative to energy expenditure (Gaston 2004). Increasing energy expenditure by increasing drag or altering buoyancy leads to more rapid depletion of oxygen stores and thus reduced dive duration. Elephant seals (*Mirounga angustirostris* (Gill, 1866)) similarly decreased dive depth and duration in response to alterations in buoyancy, although these results were not significant, possibly because of low sample sizes (Webb et al. 1998). We hypothesize that dive depths in most species are determined by prey depth and travel costs rather than by a need for achieving neutral buoyancy, except under unusual circumstances such as those outlined for loggerhead turtles (*Caretta caretta* (L., 1758)) at shallow depths where drag is

minimal as the turtles are not moving (Minamikawa et al. 2000). Several murres handicapped with 5.6 cm² blocks switched from dive bouts with deep, U-shaped dives to dive bouts with shallow, V-shaped dives. These individuals were observed bringing back amphipods, an otherwise uncommon food item at this colony, where most deliveries are of fish 10–100 times heavier than amphipods. Hence, this handicap may have caused murres to switch to a prey species that cost less to capture and bring back but also provided less energy for the chick (Gaston et al. 2003, 2005).

Rather than manipulating dive depths to achieve neutral buoyancy, murres may control air volumes to achieve neutral buoyancy for a given dive depth. Ascent rate increased

Table 2. Mean chick-rearing Thick-billed Murre dive variables from studies with TDRs of different sizes and masses.

TDR mass (g)	TDR area (mm ²)	No. of birds (<i>N</i>)	Dive depth (m)	Maximum dive depth (m)	Dive duration (s)	Maximum dive duration (s)	Source
4.5	75	17	79	88 (140)	68	153 (246)	This study ^a
12	254	2	29	76 (77)	78	132 (136)	Woo 2001 ^c
14	177	9	48	114 (136)	105	175 (196)	Mori et al. 2002
19.2	280	8	36	86 (112)	82	156 (177)	This study ^b
17	450	17			98	187 (240)	Jones et al. 2002
28.5	417	25			100	187 (249)	Woo 2001 ^c
28.5	414	14				123 (240)	Falk et al. 2000
28.5	417	3			105		Benvenuti et al. 2002
35	375	8	18	74 (107)	55	156 (224)	Croll et al. 1992
38.3	560	8	26	61 (74)	68	132 (171)	This study ^b

Note: Maximum dive depth over all individuals and maximum dive duration over all individuals are shown in parentheses.

^aUnhandicapped individuals sampled during chick-rearing period.

^bIndividuals handicapped with drag handicaps (larger sample size than for experiments reported in Results owing to inclusion of individuals for which no control period was obtained).

^cVariables derived from raw data obtained using Star-Oddi and Benvenuti TDRs.

with maximum depth. This partially represents a change in dive angle, as murrees increase dive angle during ascent from $\sim 57^\circ$ during shallow dives to $\sim 70^\circ$ during deep dives (Watanuki et al. 2006). Nonetheless, to account for a change in ascent rate from 1.25 to 1.9 m·s⁻¹ at 10 m (Fig. 1b), an increase in dive angle from $\sim 30^\circ$ to $\sim 70^\circ$ would be necessary, well beyond that shown by accelerometers (Watanuki et al. 2006), underwater video footage, or observations of shallow-diving birds seen from atop the colony. It is unlikely that the increase in ascent rate with maximum depth is due to differences in wingbeat frequency or initial ascent speed, as murrees usually do not beat their wings during ascent and they quickly achieve passive ascent speed during ascent (Lovvorn et al. 1999, 2004). This conclusion is also supported by the observation that surface pauses were anticipatory, at least for short dives, suggesting that surface pauses reflect the time needed to obtain air stores for a given dive duration (Jodice and Collopy 1999; Mori et al. 2002).

Beyond 70–90 m, air volumes appeared to be maximal, as there was no further increase in ascent rate (Fig. 1b). The ability to adjust buoyancy, with the exception of negative buoyancy beyond the point where air stores were maximized, may also explain why we saw a reduction in ascent rates with negatively buoyant handicaps but no change in ascent rates with positively buoyant handicaps. Sato et al. (2002), using passive ascent models and accelerometer data, concluded that penguins control air volumes to regulate buoyancy. Wilson (2003) and Wilson et al. (2003), using airflow loggers attached to the mouth, showed that spheniscid penguins actively control inhaled air volume depending on the depth of the subsequent dive. Metabolic rate decreases with dive depth in benthic-feeding cormorants and they may also control inhaled air volumes (Enstipp et al. 2006).

No avian study has yet been able to separate increased air volume for neutral buoyancy at depth from increased air intake for increased dive duration at depth. For murrees, ascent rates increased approximately linearly with dive depth <60 m (roughly constant spacing above 70 m in Fig. 1b) and surface pause duration increases linearly with dive duration for short dives (Croll et al. 1992; Mori et al. 2002), suggesting that air stores may track dive duration, which increases linearly with depth, rather than buoyancy,

which increases non-linearly with depth. We conclude that air stores were likely manipulated to achieve a compromise between sufficient oxygen stores for a given dive depth and minimal costs associated with buoyancy. Turtles, which dive for long periods to shallow depths, control air volumes to achieve neutral buoyancy (Milsom 1975; Minamikawa et al. 1997). Ascent rates of murrees did not increase in the top 20 m during deep dives (Gaston 2004; Fig. 1b). This result suggests that murrees reduce ascent rates by changing dive angle, air stores, or wing posture, presumably to reduce the risk of decompression sickness (Croll et al. 1992). Other deep-diving vertebrates also exhibit shallow-water slowdown, including penguins (Kooyman et al. 1971; Sato et al. 2002) and fur seals (Hooker et al. 2005).

Deep divers from many taxa increase descent and (or) ascent rates during dives to greater depths to maximize bottom time (eiders: Heath et al. 2006; penguins: Cherel et al. 1999; Charrassin et al. 2002; seals: Beck et al. 2000; whales: Hooker and Baird 1999; Martin and Smith 1999; Laidre et al. 2003; Watwood et al. 2006). Murrees increased ascent rate, but not descent rate, during dives to greater depths. As murrees beat their wings much more frequently during descent than ascent, this difference suggests that ascent rates are regulated by buoyancy and descent rates by contraction frequency. Descent rate consistently increased with depth from 1.2 to 1.8 m·s⁻¹, a pattern very similar to that shown in Svalbard murrees (Watanuki et al. 2003; Lovvorn et al. 2004). These speeds exceed the minimum cost of transport speed but are fairly similar, except at very shallow depths, to those predicted by a model presented by Lovvorn et al. (1999, Fig. 6) based on the assumption of constant work per stroke and wingbeat frequency during descent. The contraction frequency of auk wing muscle is efficient over only a narrow range of speeds (Lovvorn and Liggins 2002; Elliott et al. 2004; Elliott and Gaston 2005), and consequently descent rates are chosen to maximize physiological (e.g., muscle contraction) rather than mechanical (e.g., total energy required to pull the body fuselage to a given depth) efficiency (Lovvorn et al. 1999, 2004; Lovvorn 2001; Watanuki et al. 2003). Mechanical inefficiency may also be beneficial because the heat generated may contribute to thermoregulation (Handrich et al. 1997; Lovvorn et al. 1999;

Heath et al. 2006). Descent rate decreased when mass was increased by adding handicaps, possibly because an increase in inertia reduced instantaneous acceleration or contraction efficiency, although it is equally possible that the decrease in descent rate was due to yaw introduced by the handicap.

Device effects

This study suggests that attachment of devices that increase drag or alter buoyancy also alter foraging behaviour, including dive depth, dive duration, swim speeds, and possibly diet. The decreasing size of data-logging devices used on murres, from the 32 g back-mounted TDRs used by Croll et al. (1992) to the 4.5 g leg-mounted TDRs used in this study, likely explains why maximum dive depth and dive duration reported for murres have steadily increased since Croll et al.'s (1992) original study (Table 2), assuming data from a few anomalously deep capillary tubes are false (Croll et al. 1992). Average and maximum recorded depth and dive duration have increased as the size of the TDR deployed at our Coats Island study site has decreased (Table 2). The leg-mounted TDRs used in this study showed no effect on provisioning rate or adult mass loss in comparison with individuals without TDRs, in contrast to all previous studies of murres that have quantified these variables (Wanless et al. 1988; Croll et al. 1992; Watanuki et al. 2001; Hamel et al. 2004; Paredes et al. 2004). Small ventral or internal attachments, which have been used successfully in other species (cf. Ballard et al. 2001), affect behaviour of murres and other alcids (Meyers et al. 1998; Hatch et al. 2000; Tremblay et al. 2003). Furthermore, neutrally buoyant handicaps attached to the legs had no measurable effect on dive variables, whereas neutrally buoyant devices attached to the backs did. Consequently, the leg-attachment method appears to be the best available for murres.

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