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

Kyle H. Elliott, Gail K. Davoren, and Anthony J. Gaston

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 cm^2; n = 8) or 6% (5.6 cm^2; 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 cm^2; n = 8) ou de 6% (5,6 cm^2; 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.

[Traduit par la Rédaction]

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.

Received 16 December 2006. Accepted 26 January 2007. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 22 March 2007.

K.H. Elliott[1] **and G.K. Davoren.** Department of Zoology, Z320 Duff Roblin Building, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.
A.J. Gaston. Canadian Wildlife Service, National Wildlife Research Centre, Carleton University, Ottawa, ON K1A 0H3, Canada.

[1]Corresponding author (e-mail: urialomvia@gmail.com).

 doi:10.1139/Z07-012

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 (Pennycuick 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. 2003*a*, 2003*b*; 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 (murres: 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 murres 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 murres 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 murres 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 murres 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.

Murres 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 murres 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 ± 1 cm^3. The negatively buoyant handicaps (mass = 22.5 ± 0.9 g) were filled with lead shot and then sealed with a wooden cork, epoxy, and duct tape. The positively buoyant handicaps (mass = 7.5 ± 0.2 g) were sealed with a wooden cork, epoxy, and duct tape. The neutrally buoyant handicaps were left unsealed and weighed 15.0 ± 0.1 g when filled with water. Thus, the total buoyant force exerted by these handicaps was 0.075 ± 0.01 N downwards (negatively buoyant), 0.00 ± 0.01 N (neutrally buoyant), and 0.075 ± 0.01 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 ± SE. We analysed only dives with maximum depth >3 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 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 m excluded, as murres often do not forage during shallow dives (Croll et al. 1992). Because analyses

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

Handicap	Depth (m)	Duration (s)	Ascent rate ($m \cdot s^{-1}$)	Descent rate ($m \cdot s^{-1}$)
B+ (n = 10)	19±9*	26±11*	0.06±0.05	0.12±0.06*
B– (n = 11)	7.9±3.0*	21±7*	0.13±0.05*	0.17±0.05†
B0 (n = 9)	4.4±8.8	–0.6±12.0	0.06±0.05	0.01±0.02
2.8 cm^2 (n = 8)	12±5*	9.1±6.8	0.13±0.06*	0.13±0.05*
5.6 cm^2 (n = 6)	27±11*	46±14*	0.16±0.04†	0.32±0.02†

Note: B+, increased buoyancy; B–, decreased buoyancy; B0, neutral buoyancy; 2.8 cm^2, 2.8 cm^2 cross section neutral buoyancy; 5.6 cm^2, 5.6 cm^2 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 ± 11 g, t = –3.27, df = 8, P = 0.006; neutral buoyancy: 23 ± 7.6 g, t = –3.02, df = 9, P = 0.007; positive buoyancy: 52 ± 24 g, t = –2.19, df = 6, P = 0.04; 2.8 cm^2 drag: 36 ± 11 g, t = –3.22, df = 6, P = 0.009; 5.6 cm^2 drag: 69 ± 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 ± 3.40 feeds per day; mates: 5.04 ± 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 ± 2.29 feeds per day; no-TDR birds: 3.12 ± 2.64 feeds per day; paired t = 1.85, df = 24, P = 0.96).

Four out of 14 individuals with 2.8 cm^2 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 cm^2 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.

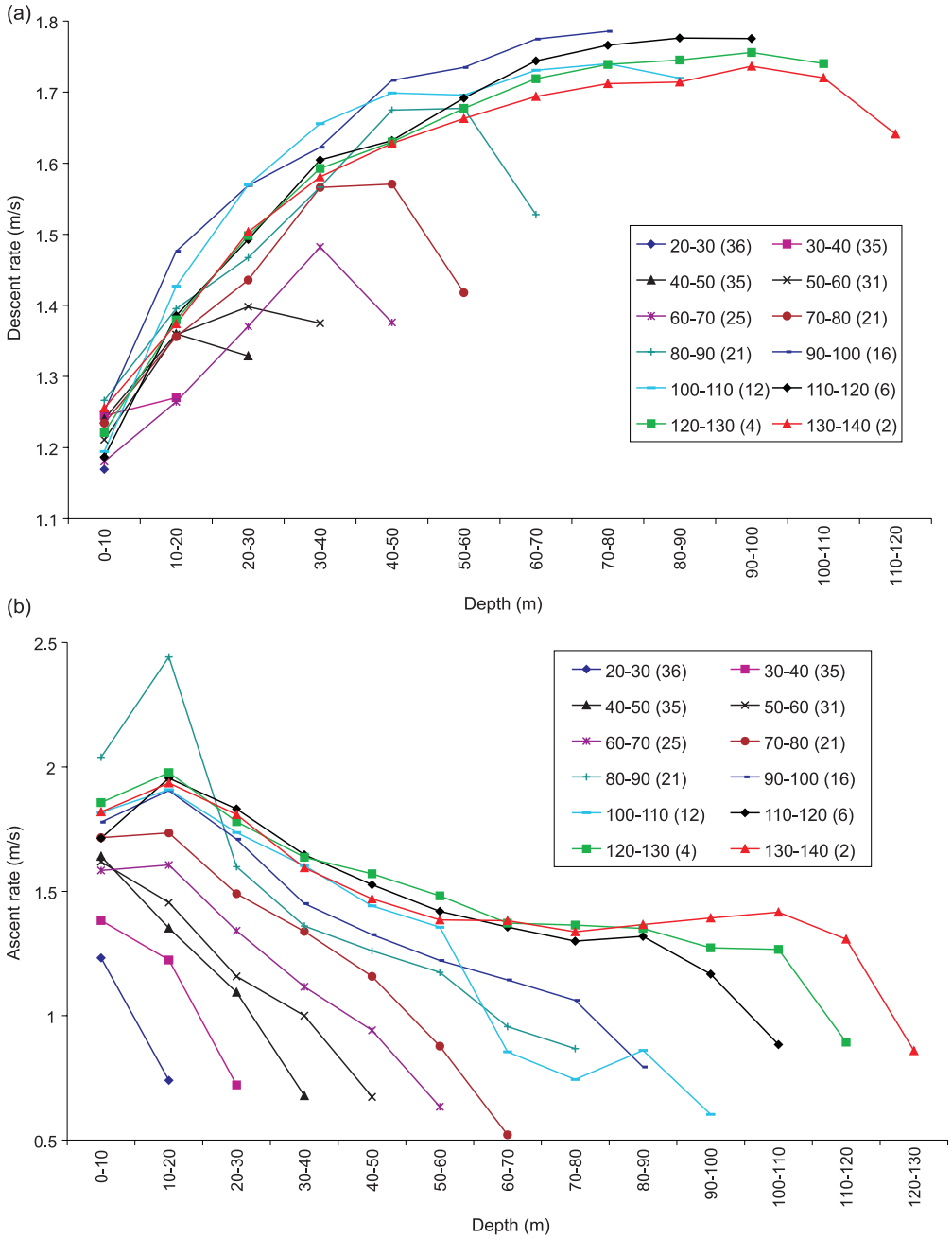
Overall, succeeding surface pauses (individual dive basis: R^2 = 0.49; individual murre basis: R^2 = 0.90) correlated just as well as preceding surface pauses (R^2 = 0.50 and 0.90) with dive duration. Succeeding surface pauses (individual dive basis: R^2 = 0.56; individual murre basis: R^2 = 0.90) also 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 cm^2 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 (*N*)	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.

[a]Unhandicapped individuals sampled during chick-rearing period.

[b]Individuals 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).

[c]Variables derived from raw data obtained using Star-Oddi and Benvenuti TDRs.

with maximum depth. This partially represents a change in dive angle, as murres increase dive angle during ascent from ~57° during shallow dives to ~70° during deep dives (Watanuki et al. 2006). Nonetheless, to account for a change in ascent rate from 1.25 to 1.9 $m \cdot s^{-1}$ at 10 m (Fig. 1*b*), an increase in dive angle from ~30° to ~70° 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 murres 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. 1*b*). 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 murres, ascent rates increased approximately linearly with dive depth <60 m (roughly constant spacing above 70 m in Fig. 1*b*) 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 murres did not increase in the top 20 m during deep dives (Gaston 2004; Fig. 1*b*). This result suggests that murres 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). Murres increased ascent rate, but not descent rate, during dives to greater depths. As murres 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 $m \cdot s^{-1}$, a pattern very similar to that shown in Svalbard murres (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.

Acknowledgements

We thank A. Ronston for her help in the field. K. Woo provided practical guidance and help that were instrumental in making this project a success. S. Benvenuti and K. Woo deployed the Benvenuti and Star-Oddi TDRs described in Table 2, and S. Benvenuti kindly provided dive excerpts. J. Nakoolak helped with construction of handicaps when he was not busy keeping us safe from bears. A. Fromevitch, K. Hedges, and P. Turko helped with data compilation. B.B. Harter, J.R. Lovvorn, K.L. Campbell, and R.A. MacArthur provided valuable comments on earlier versions of this manuscript. K.H.E. benefited from funding provided by Arctic Institute of North America Grant-in-aid, Dr. Andrew Taylor Northern Studies Research Award, Frank M. Chapman Memorial Fund, Mountain Equipment Co-op Studentship, NSERC Postgraduate (M) Award, NSERC Northern Research Internship, Northern Scientific Training Program, and Society of Canadian Ornithologists/Bird Studies Canada Taverner Award. The Canadian Wildlife Service Migratory Birds Division, the Polar Continental Shelf Project, and the University of Manitoba also funded this project. R. Armstrong at the Nunavut Research Institute, M. Mallory at the Canadian Wildlife Service Northern Research Division, and C. Eberl at the Canadian Wildlife Service in Ottawa provided logistical support. This project was completed as part of the M.Sc. requirements at the University of Manitoba for K.H.E. Finally, we would like to thank the birds on the "T" ledges for their cooperation — this project would not have been possible without them.

References

Ballard, G., Ainley, D.G., Ribic, C.A., and Barton, K.R. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. Condor, **103**: 481–490. doi:10.1650/0010-5422(2001)103[0481:EOIAAO]2.0.CO;2.

Bannasch, R., Wilson, R.P., and Culik, B. 1994. Hydrodynamic aspects of design and attachment of back-mounted devices in penguins. J. Exp. Biol. **194**: 83–96.

Beck, C.A., Bowen, W.D., and Iverson, S.J. 2000. Seasonal changes in buoyancy and diving behaviour of adult grey seals. J. Exp. Biol. **203**: 2323–2330.

Benvenuti, S., Bonadonna, F., Dall'Antonia, L., and Gudmundsson, G.A. 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. Auk, **115**: 57–66.

Benvenuti, S., Dall'Antonia, L., and Falk, K. 2002. Diving behaviour differs between incubating and brooding Brünnich's guillemots, *Uria lomvia*. Polar Biol. **25**: 474–478.

Boyd, I.L., Lunn, N.J., and Burton, T. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. J. Anim. Ecol. **60**: 577–592.

Charrassin, J.-B., Le Maho, Y., and Bost, C.-A. 2002. Seasonal changes in the diving parameters of king penguins (*Aptenodytes patagonicus*). Mar. Biol. (Berl.), **141**: 581–589.

Cherel, Y., Tremblay, Y., Guinard, E., and Georges, J.Y. 1999. Diving behaviour of female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, during the brooding period at Amsterdam Island (Southern Indian Ocean). Mar. Biol. (Berl.), **134**: 375–385.

Croll, D.A., and McLaren, E. 1993. Diving metabolism and thermoregulation in common and thick-billed murres. J. Comp. Physiol. [B], **163**: 160–166.

Croll, D.A., Osmek, S.D., and Bengston, J.L. 1991. An effect of instrument attachment on foraging trip duration in chinstrap penguins. Condor, **93**: 777–779. doi:10.2307/1368216.

Croll, D.A., Gaston, A.J., Burger, A.E., and Konnoff, D. 1992. Foraging behaviour and physiological adaptation for diving in thick-billed murres. Ecology, **73**: 344–356. doi:10.2307/1938746.

Culik, B.M., Bannasch, R., and Wilson, R. 1994. External devices on penguins: how important is shape? Mar. Biol. (Berl.), **118**: 353–357.

Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003*a*. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Mar. Ecol. Prog. Ser. **256**: 229–242.

Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. 2003*b*. Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol. Monogr. **73**: 463–481.

Elliott, K.H., and Gaston, A.J. 2005. Flight speeds of seabirds: a test of Norberg's hypothesis. Ibis, **147**: 783–789. doi:10.1111/j.1474-919x.2005.00462.x.

Elliott, K.H., Hewett, M., Kaiser, G.W., and Blake, R.W. 2004. Flight energetics of the Marbled Murrelet, *Brachyramphus marmoratus.* Can. J. Zool. **82**: 644–652. doi:10.1139/z04-031.

Enstipp, M.R., Grémillet, D., and Jones, D.R. 2006. The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). J. Exp. Biol. **209**: 845–859. doi:10.1242/jeb.02064.

Falk, K., Benvenuti, S., Dall'Antonia, L., Kampp, K., and Ribolini, A. 2000. Time allocation and foraging behaviour of chick-rearing Brünnich's guillemots *Uria lomvia* in high-arctic Greenland. Ibis, **142**: 82–92.

Fish, F.E. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. J. Exp. Biol. **137**: 157–173.

Fish, F.E. 1993. Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). J. Exp. Biol. **185**: 179–193.

Fothergill, A. (*Producer*). 2001. Frozen seas. *In* The blue planet: seas of life (Part I) [DVD]. BBC Warner, London.

Gaston, A.J. 2004. Seabirds: a natural history. Yale University Press, New Haven, Conn.

Gaston, A.J., Woo, K., and Hipfner, J.M. 2003. Trends in forage fish populations in northern Hudson Bay since 1981, as determined from the diet of nestling thick-billed murres *Uria lomvia*. Arctic, **56**: 227–233.

Gaston, A.J., Gilchrist, H.G., and Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brünnich's guillemot (*Uria lomvia* L.). J. Anim. Ecol. **74**: 832–841. doi:10.1111/j.1365-2656.2005.00982.x.

Gessaman, J.A., and Nagy, K.A. 1988. Transmitter loads affect flight speed and metabolism of homing pigeons. Condor, **90**: 662–668. doi:10.2307/1368356.

Graham, J.B., Gee, J.H., Motta, J., and Rubinoff, I. 1987. Subsurface buoyancy regulation by the sea snake *Pelamis platurus.* Physiol. Zool. **60**: 251–261.

Grémillet, D., and Wilson, R.P. 1999. Life in the fast lane: energetics and foraging strategies of the great cormorant. Behav. Ecol. **10**: 516–524. doi:10.1093/beheco/10.5.516.

Grémillet, D., Tuschy, I., and Kierspel, M. 1998. Body temperature and insulation in diving great cormorants and European shags. Funct. Ecol. **12**: 386–394. doi:10.1046/j.1365-2435.1998.00199.x.

Hamel, N.J., Parrish, J.K., and Conquest, L.L. 2004. Effects of tagging on behaviour, provisioning, and reproduction in the Common Murre (*Uria aalge*), a diving seabird. Auk, **121**: 1161–1171. doi:10.1642/0004-8038(2004)121[1161:EOTOBP]2.0.CO;2.

Handrich, Y., Bevan, R.M., Charrassin, J.-B., Butler, P.J., Putz, K., Woakes, A.J., Lage, J., and Le Maho, Y. 1997. Hypothermia in foraging king penguins. Nature (London), **388**: 64–67. doi:10.1038/40392.

Hansen, E.S., and Ricklefs, R.E. 2004. Foraging by deep-diving birds is not constrained by an aerobic diving limit: a model of avian depth-dependent diving metabolic rate. Am. Nat. **163**: 358–374. doi:10.1086/381943.

Harcourt, R.G., Schulman, A.M., Davis, L.S., and Trillmich, F. 1995. Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. Can. J. Zool. **73**: 678–690.

Hatch, S.A., Meyers, P.M., Mulcahy, D.M., and Douglas, D.C. 2000. Performance of implantable satellite transmitters in diving seabirds. Waterbirds, **23**: 84–94.

Hays, G.C., Metcalfe, J.D., and Wayne, A.W. 2004. The implications of lung-regulated buoyancy control for dive depth and duration. Ecology, **85**: 1137–1145.

Heath, J.P., Gilchrist, H.G., and Ydenberg, R.C. 2006. Regulation of stroke pattern and swim speed across a range of current velocities: diving by common eiders wintering in polynyas in the Canadian Arctic. J. Exp. Biol. **209**: 3974–3983. doi:10.1242/jeb.02482.

Hipfner, J.M., Gaston, A.J., and de Forest, L.N. 1997. The role of female age in determining egg size and laying date of Thick-billed Murres. J. Avian Biol. **28**: 271–278.

Hipfner, J.M., Gaston, A.J., and Smith, B.D. 2006. Regulation of provisioning rate in the Thick-billed Murre (*Uria lomvia*). Can. J. Zool. **84**: 931–938. doi:10.1139/Z06-066.

Hooker, S.K., and Baird, R.W. 1999. Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proc. R. Soc. Lond. B Biol. Sci. **266**: 671–676.

Hooker, S.K., Miller, P.J.O., Johnson, M.P., Cox, O.P., and Boyd, I.L. 2005. Ascent exhalations of Antarctic fur seals: a behavioural adaptation for breath-hold diving. Proc. R. Soc. Lond. B Biol. Sci. **272**: 355–363.

Hull, C.L. 1997. The effect of carrying devices on breeding royal penguins. Condor, **99**: 530–534. doi:10.2307/1369962.

Hustler, K. 1992. Buoyancy and its constraint on the underwater foraging behaviour of reed cormorants *Phalacrocorax africanus* and darters *Anhinga melanogaster*. Ibis, **134**: 229–236.

Jodice, P.G.R., and Collopy, M.W. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. Can. J. Zool. **77**: 1409–1418. doi:10.1139/cjz-77-9-1409.

Jones, I.L., Fraser, G.S., Rowe, S., Carr, X., and Taylor, P. 2002. Different patterns of parental effort during chick-rearing by female and male thick-billed murres (*Uria lomvia*) at a low Arctic colony. Auk, **119**: 1064–1074. doi:10.1642/0004-8038(2002)119[1064:DPOPED]2.0.CO;2.

Kato, A., Watanuki, Y., Nishiumi, I., Kuroki, M., Shaughnessy, P., and Naito, Y. 2000. Variation in foraging and parental behaviour of king cormorants. Auk, **117**: 718–730. doi:10.1642/0004-8038(2000)117[0718:VIFAPB]2.0.CO;2.

Kooyman, G.L., Drabek, C.M., Elsner, R., and Campbell, W.B. 1971. Diving behaviour of the Emperor penguin, *Aptenodytes forsteri*. Auk, **88**: 775–795.

Laidre, K.L., Heide-Jørgensen, M.P., Dietze, R., Hobbs, R.C., and Jørgensen, O.A. 2003. Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? Mar. Ecol. Prog. Ser. **261**: 269–281.

Lovvorn, J.R. 2001. Upstroke thrust, drag effects, and stroke-glide cycles in wing-propelled swimming by birds. Am. Zool. **41**: 154–165. doi:10.1668/0003-1569(2001)041[0154:UTDEAS]2.0.CO;2.

Lovvorn, J.R., and Liggins, G.A. 2002. Interactions of body shape, body size and stroke-acceleration patterns in costs of underwater swimming by birds. Funct. Ecol. **16**: 106–112. doi:10.1046/j.0269-8463.2001.00604.x.

Lovvorn, J.R., Croll, D.A., and Liggins, G.A. 1999. Mechanical *versus* physiological determinants of swimming speeds in diving Brünnich's guillemots. J. Exp. Biol. **202**: 1741–1752.

Lovvorn, J.R., Watanuki, Y., Kato, A., Naito, Y., and Liggins, G.A. 2004. Stroke patterns and regulation of swim speed and energy cost in free-ranging Brünnich's guillemots. J. Exp. Biol. **207**: 4679–4695. doi:10.1242/jeb.01331.

Martin, A.R., and Smith, T.G. 1999. Strategy and capability of wild belugas, *Delphinapterus leucas*, during deep, benthic diving. Can. J. Zool. **77**: 1783–1793. doi:10.1139/cjz-77-11-1783.

Mehlum, F., Hunt, G.L., Klusek, Z., Decker, M.B., and Nordlund, N. 1996. The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. Polar Biol. **16**: 537–547.

Mehlum, F., Watanuki, Y., and Takahashi, A. 2001. Diving behaviour and foraging habitats of Brünnich's guillemots (*Uria lomvia*) breeding in the High-Arctic. J. Zool. **255**: 413–423.

Meyers, P.M., Hatch, S.A., and Mulcahy, D.M. 1998. Effect of implanted satellite transmitters on the nesting behaviour of murres. Condor, **100**: 172–174. doi:10.2307/1369912.

Miller, P.O., Johnson, M.P., Tyack, P.L., and Terray, E.A. 2004. Swimming gaits, passive drag and buoyancy of diving sperm

whales *Physeter macrocephalus*. J. Exp. Biol. **207**: 1953–1967. doi:10.1242/jeb.00993.

Milsom, W.K. 1975. Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta c. caretta*. Copeia, 1975: 758–762. doi:10.2307/1443328.

Minamikawa, S., Naito, Y., and Uchida, I. 1997. Buoyancy control in diving behaviour of the loggerhead turtle *Caretta caretta*. J. Ethol. **15**: 109–118.

Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T., and Sakamoto, W. 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. J. Exp. Biol. **203**: 2967–2975.

Mori, Y., Yoda, K., and Sato, K. 2001. Defining dive bouts using a sequential differences analysis. Behaviour, **138**: 1451–1466. doi:10.1163/156853901317367690.

Mori, Y., Takahashi, A., Mehlum, F., and Watanuki, Y. 2002. An application of optimal diving models to diving behaviour of Brünnich's guillemots. Anim. Behav. **64**: 739–745. doi:10.1006/anbe.2002.3093.

Nowacek, D.P., Johnson, M.P., Tyack, P.L., Shorter, K.A., McLellan, W.A., and Pabst, D.A. 2001. Buoyant balaenids: the ups and downs of buoyancy in right whales. Proc. R. Soc. Lond. B Biol. Sci. **268**: 1811–1816.

Obrecht, H.H., III, Pennycuick, C.J., and Fuller, M.R. 1988. Wind tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. J. Exp. Biol. **135**: 265–273.

Paredes, R., Jones, I.L., and Boness, D.J. 2004. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. Anim. Behav. **69**: 197–208.

Park, K.J., Rosen, M., and Hedenstrom, A. 2001. Flight kinematics of the Barn Swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel. J. Exp. Biol. **204**: 2741–2750.

Pennycuick, C.J. 1997. Actual and 'optimum' flight speeds: field data reassessed. J. Exp. Biol. **200**: 2355–2361.

Rayner, J.M.V. 1999. Estimating power curves of flying vertebrates. J. Exp. Biol. **202**: 3449–3461.

Rayner, J.M.V. 2001. Mathematical modeling of the avian flight power curve. Math. Methods Appl. Sci. **24**: 1485–1514. doi:10.1002/mma.196.

Ropert-Coudert, Y., Bost, Ch.-A., Handrich, Y., Bevan, R.M., Butler, P.J., Woakes, A.J., and Le Maho, Y. 2000. Impact of externally attached loggers on the diving behaviour of the king penguin. Physiol. Biochem. Zool. **73**: 438–445. doi:10.1086/317743.

Ropert-Coudert, Y., Grémillet, D., Ryan, P., Kato, A., Naito, Y., and Le Maho, Y. 2004. Between air and water: the plunge dive of the Cape Gannet *Morus capensis*. Ibis, **146**: 281–290. doi:10.1111/j.1474-919x.2003.00250.x.

Ropert-Coudert, Y., Grémillet, D., and Kato, A. 2006. Swim speeds of free-ranging great cormorants. Mar. Biol. (Berl.), **149**: 415–422.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J.B., Bost, C.-A., Handrich, Y., and Le Maho, Y. 2002. Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? J. Exp. Biol. **205**: 1189–1197.

Shaffer, S.A. 2004. Annual energy budget and food requirements of breeding wandering albatrosses (*Diomedea exulans*). Polar Biol. **27**: 253–256. doi:10.1007/s00300-004-0593-5.

Shaffer, S.A., Costa, D.P., and Weimerskirch, H. 2003. Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. Funct. Ecol. **17**: 66–74. doi:10.1046/j.1365-2435.2003.00705.x.

Skrovan, R.C., Williams, T.M., Berry, P.S., Moore, P.W., and Davis, R.W. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. J. Exp. Biol. **202**: 2749–2761.

Taylor, S.S., Leonard, M.L., Boness, D.J., and Majluf, P. 2001. Foraging trip duration increases for Humboldt penguins tagged with recording devices. J. Avian Biol. **32**: 369–372. doi:10.1111/j.0908-8857.2001.320413.x.

Tobalske, B.W., Hedrick, T.L., Dial, K.P., and Biewener, A.A. 2003. Comparative power curves in bird flight. Nature (London), **421**: 363–366. doi:10.1038/nature01284.

Tremblay, Y., Cherel, Y., Oremus, M., Tveraa, T., and Chastel, O. 2003. Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. J. Exp. Biol. **206**: 1929–1940. doi:10.1242/jeb.00363.

Tremblay, Y., Cook, T.R., and Cherel, Y. 2005. Time budget and diving behaviour of chick-rearing Crozet shags. Can. J. Zool. **83**: 971–982. doi:10.1139/z05-085.

Truitt, L. (*Producer*). 1996. World's last great places: Arctic kingdom, life at the edge [VHS]. National Geographic Society, Washington, D.C.

Wanless, S., Harris, M.P., and Morris, J.A. 1988. The effect of radio transmitters on the behaviour of common murres and razorbills during chick rearing. Condor, **90**: 816–832. doi:10.2307/1368838.

Ward, S., Moller, U., Rayner, J.M.V., Jackson, D.M., Bilo, D., Nachtigall, W., and Speakman, J.R. 2001. Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling, *Sturnus vulgaris*. J. Exp. Biol. **204**: 3311–3322.

Watanabe, Y., Baranov, E.A., Sato, K., Naito, Y., and Miyazaki, N. 2006. Body density affects stroke patterns in Baikal seals. J. Exp. Biol. **209**: 3269–3280. doi:10.1242/jeb.02402.

Watanuki, Y., Mori, Y., and Naito, Y. 1992. Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. Polar Biol. **12**: 539–544.

Watanuki, Y., Mehlum, F., and Takahashi, A. 2001. Water temperature sampling by foraging Brünnich's Guillemots with bird-borne data loggers. J. Avian Biol. **32**: 189–193. doi:10.1034/j.1600-048X.2001.320214.x.

Watanuki, Y., Niizuma, Y., Gabrielsen, G.W., Sato, K., and Naito, Y. 2003. Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. Proc. R. Soc. Lond. B Biol. Sci. **270**: 483–488.

Watanuki, Y., Wanless, S., Harris, M., Lovvorn, J.R., Miyazaki, M., Tanaka, H., and Sato, K. 2006. Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. J. Exp. Biol. **209**: 1217–1230. doi:10.1242/jeb.02128.

Watwood, S.L., Miller, P.J.O., Johnson, M., Madsen, P.T., and Tyack, P.L. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). J. Anim. Ecol. **75**: 814–825. doi:10.1111/j.1365-2656.2006.01101.x.

Webb, P.M., Crocker, D.E., Blackwell, S.B., Costa, D.P., and Le Boeuf, B.J. 1998. Effects of buoyancy on the diving behaviour of northern elephant seals. J. Exp. Biol. **201**: 2349–2358.

Weimerskirch, H., Chastel, O., and Ackermann, L. 1995. Adjustments of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. Behav. Ecol. Sociobiol. **36**: 11–16. doi:10.1007/s002650050119.

Williams, T.M., and Kooyman, G.L. 1985. Swimming performance and hydrodynamic characteristics of harbour seals *Phoca vitulina*. Physiol. Zool. **58**: 576–589.

Williams, T.M., Friedl, W.A., Haun, J.E., and Chun, N.K. 1993. Balancing power and speed in bottlenose dolphins (*Tursiops truncatus*). Symp. Zool. Soc. Lond. **66**: 383–394.

Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.J., Horning, M., Calambokidis, J., and Croll, D.A. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. Science (Washington, D.C.), **288**: 133–136. doi:10.1126/science.288.5463.133.

Wilson, R.P. 2003. Penguins predict their performance. Mar. Ecol. Prog. Ser. **249**: 305–310.

Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E., and Nöldeke, E.C. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? Am. Nat. **140**: 179–200. doi:10.1086/285409.

Wilson, R.P., Simeone, A., Luna-Jorquera, G., Steinfurth, A., Jackson, S., and Fahlman, A. 2003. Patterns of respiration in diving penguins: is the last gasp an inspired tactic? J. Exp. Biol. **206**: 1751–1763. doi:10.1242/jeb.00341.

Woo, K. 2001. Foraging ecology of the Thick-billed Murre: patterns of prey location and selection. M.Sc. thesis, University of Ottawa, Ottawa, Ont.