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Costs of diving by wing and foot propulsion in a sea duck, the white-winged scoter

S. E. Richman · J. R. Lovvorn

Abstract Most birds swim underwater by either feet alone or wings alone, but some sea ducks often use both. For white-winged scoters (*Melanitta fusca*), we measured costs ($\dot{V}_{O_2}$) of dives to 2 m with descent by *feet only* versus *wings + feet* (only feet are used at the bottom). Dive costs repaid during the recovery period after a dive bout were an important fraction (27–44%) of total dive costs, and removing costs of extraneous surface behaviors increased resolution of differences between dive types. Scoters using *wings + feet* had 13% shorter descent duration, 18% faster descent speed, 31% fewer strokes/m, and 59% longer bottom duration than with *feet* only. The cost of time underwater for dives using *wings + feet* was 32–37% lower than with *feet only* ($P = 0.09$ to 0.15). When indirect methods were used to partition descent costs from costs of ascent and bottom phases, using *wings + feet* lowered descent cost by an estimated 34%. Thus, using *wings + feet* increases descent speed and lowers descent cost, leaving more time and energy for bottom foraging. For birds in cold water, the large savings may result from both biomechanical and thermoregulatory factors.

Keywords Bird swimming · Excess dive cost · Foot propulsion · Underwater dive cost · Wing propulsion

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Abbreviations

DRC	Dive recovery cost
EDC	Excess dive cost
MR_{dive}	Metabolic rate during a dive bout
MR_{total}	Total diving metabolic rate
RMR	Resting metabolic rate
UDC	Underwater dive cost

Introduction

Most avian divers swim underwater by either foot propulsion alone (loons, grebes, cormorants, most diving ducks) or wing propulsion alone (alcids, diving petrels, shearwaters, penguins). In mammals, birds, and reptiles, wing (or foreflipper) propulsion is reported to generate greater thrust and speed per unit effort (Davenport et al. 1984; Baudinette and Gill 1985; Schmid et al. 1995; Fish 1996). This difference is generally attributed to higher hydrodynamic efficiency of lift-based versus drag-based propulsors (Weihs and Webb 1983; Daniel and Webb 1987; but see Johansson and Norberg 2001). The difference might also result from higher instantaneous speeds required by drag-based foot propulsion; unlike wings, feet can generate no thrust during retraction, so higher speed is needed during the power phase to achieve the same mean speed (Lovvorn and Liggins 2002). Because drag increases nonlinearly with increasing speed, higher speeds during the power phase of foot propulsion can increase overall drag on the body during the stroke (Lovvorn 2001; Lovvorn and Liggins 2002). However, lift-based propulsion may require higher mean speeds and longer distance per stroke to develop adequate circulation around the wings (Rayner et al. 1986; Tobalske 2000). Perhaps because of this

constraint, wing propulsion used during descent is commonly supplemented or replaced by foot propulsion during sustained hovering at the bottom (Duffy et al. 1987). Although most diving duck species use only feet throughout dives, some deep-diving sea ducks (Mergini), which use only feet at the bottom, use their wings as well as feet during descent (review in Lovvorn 1991). This pattern suggests that during long descents, wing propulsion has important benefits.

Work against high buoyancy might also be an important reason to use both wings and feet. During descent, volumes of air in the respiratory system and plumage are compressed with increasing depth underwater, so that work against the buoyancy of air during descent and bottom foraging also changes with depth (Lovvorn and Jones 1991b, 1994; Wilson et al. 1992). For large-bodied sea ducks like eiders and scoters, which have higher buoyancies (22–28%) than predicted for other ducks (Lovvorn and Jones 1991a), work against buoyancy is a primary energy concern at shallow depths. This factor may favor use of both wings and feet to overcome buoyancy over shallow parts of a dive.

Trade-offs in benefits of these diving modes may be important to energy balance (Lovvorn and Gillingham 1996) or to optimization of foraging behavior (Guillemette et al. 2004; Heath et al. 2007). Sea ducks such as eiders (*Somateria* spp.) and long-tailed ducks (*Clangula hyemalis*) dive for benthic prey at depths of <1 m on some inland breeding areas and up to 70 m or more during winter (Schorger 1957; Taylor 1986; O'Connell 2001; Lovvorn et al. 2003). For white-winged scoters (*Melanitta fusca*), typical dive depths during the annual cycle range from <1 to 17 m (Hirsch 1980). Breeding ponds can have a complex canopy of submersed vegetation (Heglund 1992), whereas wintering areas are typically deep lakes, coastal bays, or open ocean that often lack physical habitat structure above the bottom. Thus, descent distances, work against buoyancy, and the need to maneuver in complex habitats vary greatly throughout the annual cycle, with possible advantages of foot propulsion alone in some situations and addition of wing propulsion in others.

To date, however, the energetics of wing and foot propulsion have been compared only between species differing substantially in body size and shape, surface smoothness, and even physiology, e.g. dabbling ducks versus small penguins (Baudinette and Gill 1985), cormorants versus much larger penguins (Culik et al. 1994 in Schmid et al. 1995), freshwater versus marine turtles (Davenport et al. 1984), and muskrats (*Ondatra zibethicus*) versus sea lions (Fish 1996). Our question for this study was *what are the energy costs of diving for a sea duck using foot propulsion alone vs. wing and foot propulsion together during descent?* To address this

question, we measured costs of voluntary dives with descent by *feet only* versus *wings + feet* in the same species (white-winged scoters) under the same experimental conditions, thereby controlling for many differences that can confound such comparisons.

Another factor that confounds comparisons among species in different studies is the method of calculating dive costs measured by respirometry. Reports vary in whether they account for dive costs repaid during the recovery period of elevated metabolism after dive bouts, and whether they include extraneous surface behaviors between dives within a bout in the cost of diving. Thus, in addition to presenting data on costs of diving by *feet only* versus *wings + feet* in the same species, we clearly define the different methods of calculating dive costs and their consequences for detecting and comparing differences.

Materials and methods

Experimental animals

For respirometry, six white-winged scoters (three male, three female, mean body mass 1.092 kg) were selected from a captive flock reared from eggs collected at Redberry Lake, Saskatchewan, Canada in 2000. Scoters were at least 4 years old when diving experiments began. When not involved in experiments, birds were housed outdoors at the University of Wyoming in a predator-proof pen 9 m long × 1.5 m wide × 2 m high, with continuous flow-through of water 0.3 m deep at 7–10°C. Before experiments, subjects were moved indoors (simulated natural photoperiod) to a net-covered fiberglass tank 4 m long × 1 m wide × 1 m deep, with continuous flow-through of water 25 cm deep at 7–10°C. Outside of experiments, the birds were fed ad libitum Mazuri® Sea Duck Diet (21.5% crude protein, 5.0% crude fat, 4.5% crude fiber) supplemented with Vionate vitamin powder (E.R. Squibb and Sons, Jemar Pet Supply, Rising Sun, MD, USA).

Scoters were trained to dive in a Plexiglas®-fronted tank (1.55 m long × 0.73 m wide × 2 m water depth) at water temperature of 9°C for at least 3 weeks before experiments. Birds were encouraged to dive by placing thawed *Macoma balthica* clams (including shells) in a metal tray at the bottom of the tank. To avoid possible effects of elevated metabolism after a large meal due to the heat increment of feeding (Kaseloo and Lovvorn 2003, 2005, 2006), only 50 clams (18–24 mm long, ∼ 19 kJ total) were offered on each experimental day. Before experimental runs, all birds were allowed to air-dry in a wire cage for 2 h before weighing (Lovvorn et al. 1991), and were fasted overnight in the dive tank for at least 12 h.

Respirometry

In the dive tank, the water surface was covered with a horizontal wire mesh barrier around a pyramidal respirometry chamber (base length 47 cm, height 44 cm, volume 36 l) which was submerged to 2 cm to form a tight seal with the water surface. To reduce anxiety and encourage diving by some individuals, a non-experimental cohort scoter was placed within a mesh enclosure at the surface of the water (Fig. 1, setup adapted from Kaseloo and Lovvorn 2003). Air was drawn through the chamber at a rate of 15–20 l/min by a vacuum pump. Out-flowing air was dried through a column of anhydrous calcium sulfate (Drierite®) and passed through a flow meter (model GFM 37, Aalborg Instruments, Orangeburg, NY, USA). A sub-sample of out-flowing air ($\sim$100 ml/min) was drawn through an oxygen analyzer (model S3/A I, Ametek, Pittsburg, PA, USA) and an infrared carbon dioxide analyzer (model AR-411, Anarad, Santa Barbara, CA, USA). Any drift in gas analysis was accounted for by recalibrating the gas analyzers at the beginning and end of each experimental run. Before experiments, the oxygen analyzer was standardized against ambient air (20.95% O_2) and a high purity air mixture (20.2% O_2, 0.8% CO_2, 79.0% N_2; U.S. Welding, Denver, CO, USA) by manually switching the inlet line for at least 5 min for each calibration. The entire respirometry system was tested for leaks by the nitrogen dilution technique described by Fedak et al. (1981) at least once per week during experiments.

Readings of time, air temperature, flow rate, and concentrations of O_2 and CO_2 were made at 30-s intervals through proportional analog outputs connected to a datalogger (model CR-10, Campbell Scientific, Logan, UT, USA; Fig. 1). All readings were means of values recorded every second and averaged for each 30-s interval. If a single dive occurred between two 30-s intervals, we included both intervals in the calculation of metabolic rate during the dive about (MR_{dive}) for that dive to include the pre-dive elevation in metabolism. The dive recovery cost (DRC) for that dive bout would then include all the costs of recovery. (For further details and definition of variables, see Appendix.)

The effective volume of the chamber was calculated as 105 l (at a flow of 20 l/min, equation 1 of Bartholomew et al. 1981), which accounts for the washout time of the system (number of sampling intervals to reach equilibrium if no further changes in $\dot{V}_{O_2}$ were to occur), and includes the volume of the tubing between the chamber and O_2 analyzer. The lag time of the system was calculated as about 60 s, which was confirmed by perturbing the system with mixed gas to below the ambient oxygen level and measuring the time to the first deflection on the O_2 analyzer. All gas volumes were converted to STPD.

Aerobic costs of diving were determined from the rate of oxygen consumption in open-flow respirometry by the protocols of Kaseloo and Lovvorn (2003, 2005, 2006). In brief, the concentrations of O_2 and CO_2 in the dome were measured continuously along with flow rate, and the rate of oxygen consumption ($\dot{V}_{O_2}$) calculated with equation 3a of Withers (1977). Estimates of $\dot{V}_{O_2}$ for each 30-s interval were calculated by the method of Bartholomew et al. (1981) based on flow rate, sampling interval, and effective volume of the chamber. For resting, swimming, and preening, we transformed $\dot{V}_{O_2}$ (ml O_2/s) to Joules and Watts by the caloric equivalent corresponding to the respiratory quotient (RQ = CO_2 produced / O_2 consumed)

Fig. 1 Respirometry apparatus for white-winged scoters in the dive tank (*solid line* air flow, *dashed line* air sample, *dotted line* analog outputs to datalogger)
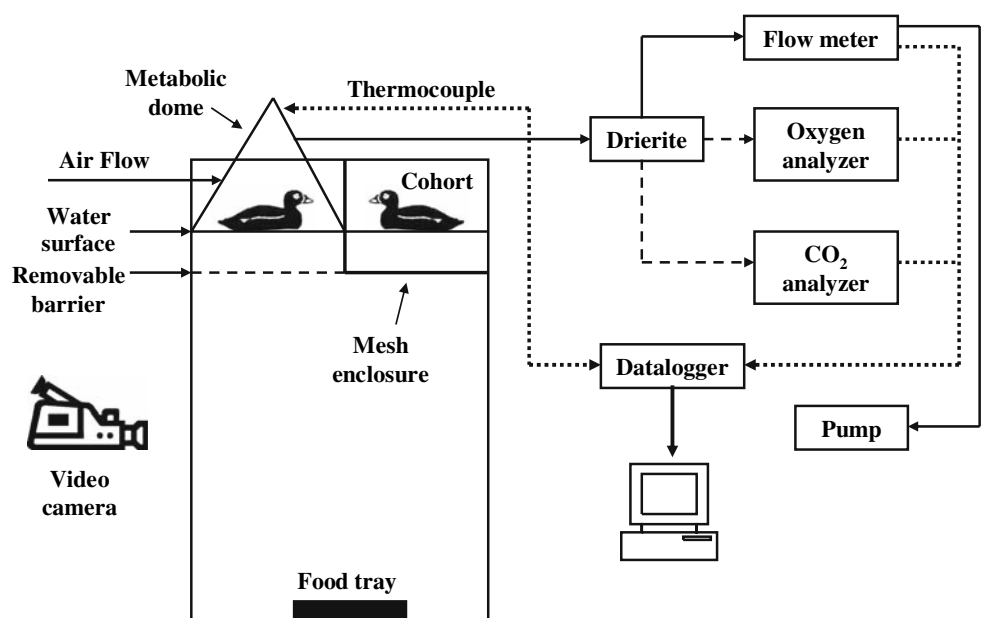
measured for each bird for each experimental day. We used conversion factors of 19.7, 20.1, and 20.3 J/ml O_2 for RQ of 0.7, 0.8, and 0.9, respectively (Schmidt-Nielsen 1997).

Analyses of behavior

All activities were videotaped (Panasonic model WV-CP234) throughout experiments. Surface behaviors were classified into three categories: (1) resting: quietly floating on the water surface with head down or tucked under the wing, or one leg tucked against the body, (2) preening: manipulating the plumage with the bill, and (3) swimming: sporadic or continuous paddling. We categorized dives into two types according to locomotor mode during descent: (1) *feet only*: foot-propelled with wings completely tucked against the body, and (2) *wings + feet*: wing strokes accompanied by foot strokes for the entire descent. Dive bouts analyzed contained only one of these dive types.

Metabolic costs of surface behaviors (resting, preening, swimming) for birds floating on water at 9°C were measured at the beginning of each experimental day. A horizontal wire mesh barrier placed 10 cm below the birds prevented diving for at least 2 h. Resting metabolic rate (RMR, for abbreviations see Appendix) for a bird floating quietly on the water was measured as the lowest 10-min average of $\dot{V}_{O_2}$ during a period of at least 30 min. We measured energy costs of preening (MR_{preen}) and swimming (MR_{swim}), which include resting metabolism, during periods when a given behavior lasted >5 min at times when there was no diving. For example, preening after a dive was not used to calculate MR_{preen}, as it would include post-dive recovery metabolism.

For individual dives by each bird, durations of descent, bottom foraging, and ascent were measured from video films with a stopwatch. Hind-limb stroke frequency was counted during descent and bottom phases for the different dive types (*feet only* vs. *wings + feet*); during descent by *wings + feet*, foot and wing strokes were simultaneous. Stroke rates for descent and bottom phases were calculated as the number of hind-limb strokes divided by the duration of the dive phase, and were used to calculate the number of strokes per vertical meter. Vertical speed (m/s) was calculated as descent duration divided by water depth (2 m).

Analyses of dive cost

Because scoters often used dives by *feet only* and *wings + feet* within the same dive bout, not all dive bouts were included in analyses. Also, levels of surface activity after a dive bout were quite variable. In some cases, birds used both dive types within the same bout, or non-diving

surface activities such as preening were continued for extended periods after a bout. As a result, only bouts in which birds used the same descent mode for all dives in the series, and for which $\dot{V}_{O_2}$ returned to RMR within 5 min of the end of the bout, were retained for analyses.

For isolated dives or dive bouts (multiple dives in succession with surface intervals <90 s), we calculated the mean rate of oxygen consumption for the total time (t_{total}) as $\dot{V}_{O_2}$ from the 30-s interval before submergence for the first dive in a bout until the bird returned to resting levels after the bout ($\dot{V}_{O_2 total}$, Fig. 2; see Appendix for definition of variables). Total dive cost was divided into two parts: (1) $\dot{V}_{O_2}$ during the dive bout ($\dot{V}_{O_2 DB}$), measured from 30 s before submergence for the first dive in a bout until the bird surfaced after the last dive in a bout (t_{DB}), and (2) $\dot{V}_{O_2}$ during the dive recovery period ($\dot{V}_{O_2 DRC}$), measured from the end of the last dive in a bout until $\dot{V}_{O_2}$ returned to resting levels (t_{DRC}). For determining the end of the recovery period, we used RMR obtained on the same day for a given individual. As reported by others (Woakes and Butler 1983; Enstipp et al. 2001), avian divers typically show an anticipatory period of elevated $\dot{V}_{O_2}$, heart rate, and respiratory rate during the 30-s period before the first dive in a bout, presumably to load oxygen stores; we therefore included this period of elevated metabolism in our analysis.

The cost of diving during a dive bout, MR_{dive} (ml O_2/s), was calculated as mean $\dot{V}_{O_2 DB}$ for the duration of the dive bout (t_{DB}) minus costs of preening (MR_{preen}) and
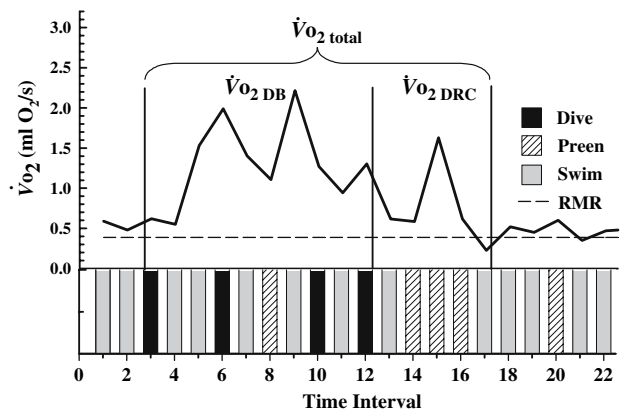
Fig. 2 Oxygen consumption ($\dot{V}_{O_2}$) during different periods of a dive bout, showing $\dot{V}_{O_2 DB}$ ($\dot{V}_{O_2}$ for the dive bout to calculate MR_{dive}) from 30 s before initial submergence until surfacing at the end of the last dive in the bout, $\dot{V}_{O_2 DRC}$ (for calculating dive recovery cost, DRC) from the last surfacing until $\dot{V}_{O_2}$ returns to resting metabolic rate (RMR), and $\dot{V}_{O_2 total}$ (for calculating MR_{total} which includes both MR_{dive} and DRC). Lower panel shows examples of predominant behaviors during each 30-s interval. Costs of preening and swimming at the surface (including RMR during those behaviors), measured at times with no diving, were applied to data in the lower panel and subtracted from $\dot{V}_{O_2}$ before MR_{dive} and DRC were calculated

swimming (MR_{swim}) which include resting metabolism during those behaviors:

$$MR_{dive} = [(\dot{V}_{O_2DB} \times t_{DB}) - (MR_{preen} \times t_{DB\ preen}) \\ - (MR_{swim} \times t_{DB\ swim})]/t_{DB} \quad (1)$$

Dive recovery cost, DRC (ml O_2/s), was calculated as mean $\dot{V}_{O_2DRC}$ from the end of the last dive in a bout until $\dot{V}_{O_2}$ returned to RMR (t_{DRC}), minus costs of preening and swimming which include resting metabolism during those behaviors:

$$DRC = [(\dot{V}_{O_2DRC} \times t_{DRC}) - (MR_{preen} \times t_{DRC\ preen}) \\ - (MR_{swim} \times t_{DRC\ swim})]/t_{DRC} \quad (2)$$

For Eqs. 1 and 2, the predominant behavior (resting, preening, or swimming) over each 30-s interval was recorded while the bird was at the surface between dives and during the recovery period. Costs of preening and swimming were measured during times with no diving to avoid including elevated metabolism due to diving itself. For example, in Fig. 2, $\dot{V}_{O_2}$ during preening in the recovery period (interval 14–16) is elevated compared to the cost during preening after the recovery period (interval 20). Thus, measuring the cost of preening during the recovery period would grossly overestimate preening cost as it would include dive recovery cost as well. Further, including the cost of preening during the dive recovery would overestimate DRC.

Total cost, MR_{total} (ml O_2/s), during the dive bout and subsequent recovery (t_{total}) was calculated by weighting MR_{dive} and DRC by the duration of the dive bout (t_{DB}) and DRC (t_{DRC}), and dividing by the total duration (t_{total}):

$$MR_{total} = [(MR_{dive} \times t_{DB}) + (DRC \times t_{DRC})]/t_{total} \quad (3)$$

Excess dive cost, EDC (ml O_2/s_{uw}), was defined by de Leeuw (1996) as the total rate of oxygen consumption ($\dot{V}_{O_2total}$) in excess of RMR from the onset of diving until return to RMR at the end of the recovery period, divided by time spent underwater (t_{uw}):

$$EDC = [(\dot{V}_{O_2total} - RMR) \times t_{total}]/t_{uw} \quad (4)$$

EDC includes the cost of surface behaviors between dives and during the recovery period, and as a result can appreciably overestimate the cost of diving alone. To better measure the cost of diving independent of other activities, we calculated the underwater dive cost, UDC (ml O_2/s_{uw}), as $MR_{total}(\dot{V}_{O_2}$ from 30 s before onset of first dive until return to RMR minus costs of preening and swimming including RMR during those behaviors) for the total time (t_{total}), divided by time underwater (t_{uw}).

$$UDC = (MR_{total} \times t_{total})/t_{uw} \quad (5)$$

Because UDC is calculated by subtracting costs of surface behaviors which include resting metabolism, we also calculated UDC in excess of RMR (UDC − RMR, ml O_2/s_{uw}) for the period spent underwater by subtracting RMR only during the time spent underwater:

$$UDC - RMR = [(MR_{total} \times t_{total}) - (RMR \times t_{uw})]/t_{uw} \quad (6)$$

Statistics

For surface activities and for treatment groups performing dives by *feet only* versus *wings + feet*, we used repeated-measures analysis of covariance (ANCOVA) with Tukey multiple mean comparisons, birds as blocks, and body mass as covariate (Proc GLM, SAS Institute 1987). This approach accounts for effects of body mass differences between groups and sexes, while avoiding potentially erroneous results of tests on ratios formed from dividing by body mass (Packard and Boardman 1999). For MR_{dive}, DRC, and MR_{total}, we also used duration of the dive bout (t_{DB}) as a covariate to account for the large difference in average duration of bouts between treatment groups. We report least squares means (population marginal means, Searle et al. 1980) and standard errors. We used t tests to examine differences between dive types in dive-phase durations, vertical speeds, and stroke rates.

Results

Costs of resting, preening, and swimming at the surface

During periods when no diving occurred, the mean RMR (±SE) of fasted white-winged scoters (mean mass 1.092 kg) floating on water at 9°C was 0.320 ± 0.018 ml O_2/s (5.91 ± 0.35 W/kg). This value is similar to that of common eiders (*Somateria mollissima*, 1.8 kg) floating quietly on much warmer water (16–25°C): 0.343 ml O_2/s (3.83 W/kg) (Jenssen et al. 1989). The $\dot{V}_{O_2}$ for preening (MR_{preen}) and swimming (MR_{swim}) measured during periods of no diving were 2.0 and 1.3 times higher than RMR while floating on water (Table 1).

Dive phase durations, stroke frequencies, and vertical speed

We analyzed video films of 202 dives by four different scoters. In 33% of these dives, descent was by *feet only* and in 19% by *wings + feet* only. The remaining 48% of dives, which had 2–3 wing strokes followed by *feet only*, were excluded from further analyses because of inconsistent use of wings by different birds within the same dive bout.

Table 1 Costs of resting (RMR), preening, and swimming for six white-winged scoters floating on water at 9°C, during periods of no diving

Behavior	Oxygen consumption (ml O₂/s)	Energy expenditure	
		(W)	(W/kg)
Resting ($n = 5$)	0.320 ± 0.018^a	6.40 ± 0.37^a	5.91 ± 0.35^a
Preening ($n = 6$)	0.654 ± 0.022^b	13.17 ± 0.43^b	12.19 ± 0.41^b
Swimming ($n = 6$)	0.419 ± 0.013^c	8.37 ± 0.25^c	7.86 ± 0.24^c

Values are least squares means $\pm$ SE from repeated measures analysis of covariance (ANCOVA) with birds as blocks and body mass as covariate. Values in the same column with different letters are significantly different (Tukey pair-wise comparisons, all $P < 0.001$)

Dives consisted of a descent phase by *feet only* or by *wings + feet*, a bottom phase, and passive ascent. At the bottom, continuous foot strokes were used to resist the upward force of buoyancy; the primary and secondary feathers of the wings were partially expanded but were not stroked, and the alula (a group of feathers extending from the bend of the wing) was extended laterally (see Brooks 1945). Ducks surfaced by stopping foot strokes and ascending passively by positive buoyancy.

For a depth of 2 m, dives by *wings + feet* had 13% shorter descent duration and 59% longer bottom duration (Table 2). During descent, dives by *wings + feet* had 18% faster vertical speed, 31% fewer strokes/m, and 19% lower stroke rate. Neither stroke rate at the bottom or duration of passive ascent differed between the two dive types.

Diving metabolism, excess dive cost, and underwater dive cost

We included 48 dive bouts (159 dives) from 4 different birds, in which 60% of dives used *feet only* and 40% used

Table 2 Dive parameters (mean $\pm$ SE) for four white-winged scoters diving to 2 m using *feet only* or *wings + feet* during descent, and P values for t tests between dive types

	Feet only	Wings + feet	P value
Descent duration (s)	6.1 ± 0.3	5.3 ± 0.1	0.04
Bottom duration (s)	7.8 ± 0.7	12.4 ± 2.4	0.07
Ascent duration (s)	4.2 ± 0.3	4.4 ± 0.4	0.41
Total dive duration (s)	18.0 ± 1.3	22.2 ± 2.1	0.08
Vertical speed, descent (m/s)	0.34 ± 0.02	0.40 ± 0.01	0.04
Strokes/m, descent	11.70 ± 0.36	8.09 ± 0.23	<0.01
Stroke rate, descent (Hz)	3.78 ± 0.15	3.08 ± 0.13	0.01
Stroke rate, bottom (Hz)	3.20 ± 0.02	3.04 ± 0.11	0.12

wings + feet during descent. Number of dives per bout was highly variable, ranging from 1 to 18 dives for *feet only* and from 1 to 22 dives for *wings + feet*. Duration of dive bouts (t_{DB}) was also highly variable, ranging from 30 to 1,140 s for *feet only* and from 30 to 1,290 s for *wings + feet*. Despite high variability, bout duration was systematically almost twice as long for *wings + feet* as for *feet only*, and was an important covariate for dive costs (Table 3). For dives 2 m deep in water at 9°C, the two dive types did not differ in duration of the recovery period after a dive bout (t_{DRC}). Although $\dot{V}_{O_2}$ was 17–28% higher for *feet only* dives during dive bouts (MR$_{dive}$), during the recovery period (DRC), and during both periods combined, no differences were significant (Table 3, $P > 0.42$). In terms of metabolic work (ml O₂), the cost during recovery was 44 ± 14% of total dive cost excluding surface behaviors for *feet only* dives, and 27 ± 18% for dives by *wings + feet*. The fraction of dive costs met during the recovery period is clearly critical to dive cost measurements.

Excess dive cost (EDC) was defined as $\dot{V}_{O_2}$ in excess of RMR from 30 s before the onset of diving until the end of the recovery period, including costs of surface activities between dives and during recovery, divided by the time spent underwater (de Leeuw 1996; Appendix). The least squares mean of EDC for dives by *wings + feet* was 37% lower than for *feet only* ($F_{1,31} = 3.01$, $P = 0.09$, EMS = 2.013; Table 4). Removing costs of surface activities (preening and swimming) from EDC to yield underwater dive cost (UDC) lowered dive costs by up to 9%, thereby improving estimates of the costs of underwater propulsion. However, removing costs of surface activities did not increase the detectability of differences between dive types (for UDC, $F_{1,31} = 2.24$, $P = 0.14$, EMS = 1.667; for UDC − RMR, $F_{1,31} = 2.32$, $P = 0.14$, EMS = 1.644). Although differences were not significant at the 0.05 level, the cost of dives by *wings + feet* was still 32 and 35% lower than for dives by *feet only* as measured by UDC and UDC – RMR (Table 4). Although the highly variable behavior of scoters underwater tends to overwhelm even large differences between means (see "Discussion"), such large differences are likely to be biologically important (Johnson 1999).

Costs of descent

We wished to partition the costs of descent versus bottom phases for scoters. These birds stroke their feet both during descent and at the bottom, so we first calculated the work of stroking during both phases combined during *feet only* dives ($W_{stroke\ feet}$) by subtracting the estimated work of passive ascent (RMR $\times$ t_{asc}) from the total work of elevated metabolism for *feet only* dives:

Table 3 Durations of dive bouts (t_{DB}) and recovery periods after dive bouts (t_{DRC}), and oxygen consumption during a dive bout (MR_{dive}), during the recovery period (DRC), and over both periods combined (MR_{total}) for four white-winged scoters diving to 2 m in water at 9°C, using descent by either *feet only* or *wings + feet*

Dive type	t_{DB} (s)	t_{DRC} (s)	MR_{dive} (ml O_2/s)	DRC (ml O_2/s)	MR_{total} (ml O_2/s)
Feet only	207.7 ± 48.9	148.8 ± 7.9	0.940 ± 0.095	0.504 ± 0.078	0.734 ± 0.064
Wings + feet	409.1 ± 127.4	147.3 ± 7.5	0.733 ± 0.190	0.405 ± 0.156	0.630 ± 0.129
P value			0.42	0.64	0.55

Variables are defined in Appendix. Values for dive costs are least squares means ± SE tested by repeated-measures analysis of covariance (ANCOVA) with birds as blocks, and body mass and bout duration as covariates. *P* values are for Tukey pair-wise comparisons

Table 4 Excess dive cost (EDC), underwater dive cost (UDC), and UDC − RMR for the time spent underwater (s_{uw}) for four white-winged scoters diving to 2 m in water at 9°C

Dive type	EDC (ml O_2/s_{uw})	UDC (ml O_2/s_{uw})	UDC − RMR_{uw} (ml O_2/s_{uw})	P_{desc} (ml O_2/s_{desc})	P_{bott} (ml O_2/s_{bott})
Feet only	5.02 ± 0.41	4.57 ± 0.37	4.26 ± 0.37	1.011	0.730
Wings + feet	3.15 ± 0.81	3.10 ± 0.74	2.78 ± 0.74	0.665	
P value	0.09	0.14	0.14		

Estimated power expended during descent (P_{desc}) and at the bottom (P_{bott}) were partitioned as described in the text. Values are least squares means ± SE tested by repeated-measures analysis of covariance (ANCOVA) with birds as blocks and body mass as a covariate. *P* values are for Tukey pairwise comparisons

$$W_{stroke\ feet} = (MR_{total\ feet} \times t_{dive\ feet}) - (RMR \times t_{asc\ feet}). \tag{7}$$

For scoters diving by *feet only*, with an $MR_{total\ feet}$ of 0.734 ml O_2/s, RMR of 0.320 ml O_2/s, average dive time ($t_{dive\ feet}$) of 18.0 s, and ascent duration ($t_{asc\ feet}$) of 4.2 s, the $W_{stroke\ feet}$ was calculated as 11.868 ml O_2 (values from Tables 1, 2, and 3). Similarly, the work of stroking for dives by *wings + feet* ($W_{stroke\ wing}$) was calculated as 12.578 ml O_2.

For foot-propelled lesser scaup diving to 2 m at 8°C in the same experimental tank, power expended was 0.907 ml O_2/s during descent and 0.654 ml O_2/s at the bottom (values include prorated DRC, Table 5 in Kaseloo and Lovvorn 2005). When power expended during the respective phases by scaup was multiplied by the mean times spent descending and at the bottom by scoters during *feet only* dives, the fraction of total work during these two stroking phases was 52% during descent and 48% at the bottom. To estimate power expended during the respective phases by scoters, we applied these percentages for scaup to the calculated work of stroking during both phases during *feet only* dives by scoters ($W_{stroke\ feet}$), and divided by durations of the respective phases:

$$P_{desc\ feet} = (0.52 \times W_{stroke\ feet})/t_{desc\ feet} \tag{8}$$

$$P_{bott} = (0.48 \times W_{stroke\ feet})/t_{bott\ feet} \tag{9}$$

where $W_{stroke\ feet}$ is the work of stroking for *feet only* dives (11.868 ml O_2), and $t_{desc\ feet}$ (6.1 s) and $t_{bott\ feet}$ (7.8 s) are the average durations of descent and bottom foraging for *feet only* dives by scoters (Table 2). For scoters diving by *feet only*, the cost of descent ($P_{desc\ feet}$) was calculated as 1.011 ml O_2/s_{desc}, and the cost of bottom foraging ($P_{bott\ feet}$) was calculated as 0.730 ml O_2/s_{bott} (Table 4).

Because scoters use only foot propulsion while at the bottom regardless of descent mode (*feet only* or *wings + feet*), we assumed that the cost at the bottom ($P_{bott\ feet}$) was the same for either mode. Therefore, the power expended during descent for a dive by *wings + feet* was

$$P_{desc\ wing} = [W_{stroke\ wing} - (P_{bott} \times t_{bott\ wing})]/t_{desc\ wing} \tag{10}$$

where $W_{stroke\ wing}$ is the work of stroking for a dive by *wings + feet* (12.578 ml O_2), and $t_{desc\ wing}$ (5.3 s) and $t_{bott\ wing}$ (12.4 s) are durations of descent and bottom foraging, for a dive by *wings + feet*. Work during the bottom phase for dives by *wings + feet* = 0.730 ml O_2/s_{bott} × 12.4 s = 9.052 ml O_2. By subtraction, the work of descent by *wings + feet* = 12.578 ml O_2 - 9.052 ml O_2 = 3.526 ml O_2 over 5.3 s, or 0.665 ml O_2/s_{desc} (Table 4). Although these estimates depend on several important assumptions, using wings in addition to feet reduced the cost of descent from 1.011 to 0.665 ml O_2/s_{desc}, or by 34%.

Discussion

Our study is the first to measure the benefits of wing propulsion relative to foot propulsion in the same species under the same experimental conditions. Dive costs repaid during the recovery period after a dive bout were an important fraction of total dive costs (27–44%), and removing costs of extraneous surface behaviors reduced measurements of dive costs by up to 9%. White-winged scoters using *wings + feet* had 13% shorter descent duration and 18% faster vertical speed than in dives using *feet only*. Because of very large variation in metabolic costs within and between individuals, average metabolic rates during the dive bout (MR_{dive}), recovery period (DRC), and both combined (MR_{total}) did not differ significantly between dive types (all $P > 0.42$), despite being 17 to 28% higher for dives by *feet only*. Costs of time underwater (EDC, UDC, UDC − RMR) were 47 to 59% higher for dives by *feet only* ($P = 0.09-0.14$). When descent costs were partitioned indirectly from costs of bottom and ascent phases, using *wings + feet* decreased descent costs by an estimated 34% relative to descent by *feet only*. Thus, using wing propulsion to supplement foot propulsion has substantial benefits to these sea ducks.

Behavioral variability in scoters

Almost all respirometry studies of dive costs in ducks have been done on the tufted duck (*Aythya fuligula*) or its very close congener the lesser scaup (Woakes and Butler 1983; Kaseloo and Lovvorn 2005, 2006). In comparison with those studies including our own in the same measurement system, variances in $\dot{V}_{O_2}$ for white-winged scoters were strikingly high. Ducks of the genus *Aythya* adapt easily to experimental conditions. In tanks like ours, *Aythya* spp. generally dive straight to the bottom with rapid and relatively constant speed (Lovvorn 1994), yielding low variance in measurements of dive costs. In contrast, in both the tank used here and much larger tanks we have used for foraging studies of scaup, eiders, and scoters (Richman and Lovvorn 2003, 2004), dive patterns of eiders and scoters differed dramatically from those of scaup. Scoters and eiders typically spiraled to the bottom with trajectories that differed widely among dives, often varying their speed and angle of descent within the same dive. Unlike scaup and tufted ducks, scoters are very nervous birds in captivity; most of our captive flock of over 30 scoters refused to dive under the respirometer, and those that did would perform only rarely and intermittently. These aspects suggest that in addition to highly variable dive behavior, metabolic rates were likely influenced by variable nervousness (anxiousness and excitability) among and within individuals. These behavioral traits of scoters appeared to result in very high variances in $\dot{V}_{O_2}$, which weakened statistical tests despite effect sizes of up to 60%.

Cost of diving, EDC, and UDC

A factor that confounds comparisons among species in different studies is the way that dive costs measured by respirometry ($\dot{V}_{O_2}$) are calculated, often for different purposes. In a study of heart rate variations, Woakes and Butler (1983) used a multiple regression approach in which $\dot{V}_{O_2}$ during intervals between individual dives is regressed on the duration of the preceding dive and the duration of the inter-dive interval. This method assumes that the cost of each dive is entirely met during the subsequent inter-dive interval, and does not account for dive costs met during the period of elevated metabolism during the recovery period after a dive bout. Such costs include replenishing oxygen stores, restoring body temperature, and eliminating anaerobic metabolites. Although measures of dive costs for birds in experimental tanks are short and rarely involve anaerobic metabolism, the dive recovery cost (DRC) during the period from the last dive in a bout until return to resting metabolic rate (RMR) has been reported to account for up to 30% of the total metabolic costs of diving (de Leeuw 1996; Kaseloo and Lovvorn 2005). In our study, DRC averaged 27% of total dive costs for dives by *wings + feet*, and 44% for dives by *feet only*. Thus, measures that do not account for costs repaid after a dive bout may grossly underestimate costs of diving.

To address this issue, de Leeuw (1996) suggested the use of excess dive cost (EDC), defined as metabolism in excess of RMR from the onset of the first dive in a bout until the end of post-bout recovery, and divided by the time underwater. However, birds typically engage in other behaviors at the surface both between dives and during the recovery period. For example, although restoring the plumage air layer may be needed after diving activities, preening is not part of the dive cost itself and is often partitioned from diving in time-activity budgets. Dive cost measurements can be further refined by subtracting the cost of surface behaviors, as we did in calculating UDC.

Although dive costs per second underwater (EDC or UDC) did not differ at $\alpha = 0.05$ between the two dive types, the energy expended was on average 37% (EDC) and 32% (UDC) lower for dives by *wings + feet* than for dives by *feet only*. Removing costs of extraneous surface behaviors, as done in calculating UDC but not EDC, lowered estimates of dive cost by up to 9%, but did not improve detectability of differences between dive types. High variances in metabolic costs both within and between individuals can overwhelm even large differences in means, so that biologically significant differences are non-significant statistically (Martinez-Abrain 2007). Decrease

of >32% in costs of time spent underwater (EDC and UDC) for dives using *wings + feet* versus *feet only* is ecologically important to the energy costs of deep-diving sea ducks.

Mechanical benefits of propulsion by *wings + feet*

In swimming mammals, birds, and reptiles, drag-based foot propulsion generally yields less thrust and speed per unit cost than lift-based wing propulsion (Davenport et al. 1984; Baudinette and Gill 1985; Schmid et al. 1995; Fish 1996). This difference is attributed to the fact that if forward speeds are high enough and stroke distances long enough for flow development around the wings, thrust can be generated with less energy by lift-based than drag-based mechanisms (Weihs and Webb 1983; Daniel and Webb 1987). Aside from the hydrodynamics of propulsors themselves, there is also the issue of drag on the body fuselage as a function of instantaneous speed throughout the stroke cycle. Lift-based propulsors can often generate thrust on both upstoke and downstroke, whereas drag-based propulsors generate thrust only during extension (power phase) and not during retraction (Davenport et al. 1984; Hui 1988; Johansson and Aldrin 2002; Lovvorn and Liggins 2002). Thus, to achieve the same mean swimming speed, drag-based swimmers must have higher instantaneous speeds during the power phase. Because drag increases nonlinearly with increasing speed, this factor can increase overall drag and costs of swimming (Lovvorn 2001).

Foot propulsion, however, may have advantages over wing propulsion when forward speeds or distance per stroke while hovering are often low or negligible, as for birds which feed mainly on the bottom or in complex, shallow habitats. Among alcids, which generally feed in the water column and swim by wings only, pigeon guillemots (*Cepphus columba*) use feet as well as wings when searching complex bottom substrates for prey (Duffy et al. 1987). Other birds that feed on the bottom or often forage in shallow, sometimes vegetated habitats, including loons, grebes, cormorants, and anhingas, do not use their wings for underwater swimming (Lovvorn 1991). Because many sea ducks forage in inland waters with dense vegetation during summer, it may be ineffective to use their wings while maneuvering along the bottom. Conversely, long-tailed ducks (*Clangula hyemalis*), which during winter are among the deepest-diving ducks and often feed on amphipods, mysids, and fish above the bottom (Robertson and Savard 2002), are the only duck reported to swim horizontally by wings only without using the feet (Snell 1985; J. P. Heath, personal communication). Our results suggest that by using *wings + feet* during descent and *feet only* at the bottom, eiders and scoters accrue benefits of lift-based propulsion during long descents, and of foot propulsion while feeding on benthic prey.

Moreover, coordination of foot strokes and wing strokes may reduce overall drag by allowing more constant instantaneous speeds throughout the stroke cycle. Recently, Heath et al. (2006) described the stroke patterns of common eiders (*Somateria mollissima*) diving in the Canadian Arctic. They found that during the upstroke the wings had a fairly low angle of attack, while during the downstroke and especially the transition between upstroke and downstroke, the angle of attack was much greater with presumably much higher drag. The recovery stroke of the feet (with the webbing closed) occurred during the upstroke of the wing, and the power stroke of the feet occurred during the transition of the wing stroke from upstroke to downstoke. This timing may avoid higher drag incurred by more unsteady thrust at the same mean speed, thereby reducing the energy cost of descent (Lovvorn 2001; Heath et al. 2006). The fact that descent power in our scoters using *wings + feet* was much lower than for *feet only* suggests the importance of this mechanism.

Wings + feet and thermal substitution

To estimate costs of descent alone for *wings + feet* versus *feet only*, we assumed that the cost of passive ascent was equal to RMR. RMR for the mean ascent duration was subtracted from MR_{total} for dives by *wings + feet* or *feet only*, to yield the cost of descent and bottom time combined. We assumed that the relative costs of descent and bottom phases for a scoter using *feet only* would resemble those of a foot-propelled lesser scaup diving to the same depth (2 m) at the same temperature (8–9°C) in the same experimental tank (Kaseloo and Lovvorn 2005). For scaup, the relative cost of descent was 52%, and of staying at the bottom 48%, of the total cost of stroking underwater. Based on the same percentages (see "Results"), the descent cost for scoters diving to 2 m at 9°C using *wings + feet* was 34% lower than for dives by *feet only*.

Given high heat loss to water at this temperature, this large energy savings might result partly from thermal substitution. Substitution is the use of heat produced by exercising muscles to replace heat lost, thereby lowering costs of thermoregulation (Paladino and King 1984; Webster and Weathers 1990, Zerba and Walsberg 1992; review in Lovvorn 2007). In foot-propelled diving ducks, this reduction can range from 43 to 90% of total heat production (Bevan and Butler 1992; Kaseloo and Lovvorn 2005, 2006). Scoters using *wings + feet* are working their large pectoral muscles in addition to leg muscles, increasing the "waste" heat of muscle inefficiency that is generated during swimming. If, as in lesser scaup, heat generated during *feet only*

dives does not replace all heat lost, additional heat produced by wing muscles may further reduce dive costs. Thus, for birds diving in cold water, benefits of wing propulsion may be thermoregulatory as well as biomechanical.

In summary, using wings in addition to feet provides important benefits, especially for birds that have high buoyancy or make long descents with sustained forward speeds. Wing propulsion increases speed and lowers power expended during descent, leaving more time and energy for foraging at the bottom.

Appendix: Definitions of variables

DRC — dive recovery cost, $\dot{V}_{O_2}$ from end of last dive in bout until return to RMR, minus costs of preening and swimming including RMR during those behaviors (ml O_2/s) $= [(\dot{V}_{O_2 DRC} \times t_{DRC}) - (MR_{preen} \times t_{DRC\,preen}) - (MR_{swim} \times t_{DRC\,swim})]/t_{DRC}$

EDC — excess dive cost, $\dot{V}_{O_2}$ from 30 s before onset of first dive until return to RMR, minus RMR for the entire period, divided by time spent underwater (ml O_2/s) $= (\dot{V}_{O_2 total} - RMR) \times t_{total}/t_{uw}$

MR_{dive} — metabolic rate from 30 s before onset of first dive until end of last dive in bout, minus costs of preening and swimming including RMR during those behaviors (ml O_2/s) $= [(\dot{V}_{O_2 DB} \times t_{DB}) - (MR_{preen} \times t_{DB\,preen}) - (MR_{swim} \times t_{DB\,swim})]/t_{DB}$

MR_{preen} — metabolic rate while preening (including RMR), during periods of no diving (ml O_2/s)

MR_{swim} — metabolic rate while swimming (including RMR), during periods of no diving (ml O_2/s)

MR_{total} — metabolic rate from 30 s before onset of first dive until return to RMR, minus cost of preening and swimming including RMR during those behaviors (ml O_2/s) $= [(MR_{dive} \times t_{DB}) + (DRC \times t_{DRC})]/t_{total}$

RMR — resting metabolic rate while floating on water, during periods of no diving (ml O_2/s)

P_{bott} — power expended at the bottom for either dive type (ml O_2/s)

$P_{desc\,feet}$ — power expended during descent for dives by *feet only* (ml O_2/s)

$P_{desc\,wing}$ — power expended during descent for dives by *wings + feet* (ml O_2/s)

t_{asc} — mean ascent duration for respective dive type (s)

t_{bott} — mean bottom duration for respective dive type (s)

t_{DB} — time from 30 s before onset of first dive until end of last dive in bout (s)

$t_{DB\,preen}$ — time spent preening during pauses between dives during a bout (s)

$t_{DB\,swim}$ — time spent swimming during pauses between dives during a bout (s)

t_{desc} — mean descent duration for respective dive type (s)

t_{dive} — mean dive duration for respective dive type (s)

t_{DRC} — dive recovery period from end of last dive in bout until $\dot{V}_{O_2}$ returns to RMR (s)

$t_{DRC\,preen}$ — time spent preening during the dive recovery period (s)

$t_{DRC\,swim}$ — time spent swimming during the dive recovery period (s)

t_{surf} — time spent at the surface between dives during the dive bout (s)

t_{total} — time from 30 s before onset of first dive until end of dive recovery period (s)

t_{uw} — time underwater during a dive bout (s)

UDC — underwater dive cost, $\dot{V}_{O_2}$ from 30 s before onset of first dive until return to RMR, minus costs of preening and swimming including RMR during those behaviors, (MR_{total}), divided by time spent underwater (ml O_2/s) $= (MR_{total} \times t_{total})/t_{uw}$

UDC − RMR_{uw} — underwater dive cost in excess of RMR for the time spent underwater (ml O_2/s) $= [(MR_{total} \times t_{total}) - (RMR \times t_{uw})]/t_{uw}$

$\dot{V}_{O_2 DB}$ — $\dot{V}_{O_2}$ from 30 s before onset of first dive in bout until end of last dive in bout (ml O_2/s)

$\dot{V}_{O_2 DRC}$ — $\dot{V}_{O_2}$ from end of last dive in bout until return to RMR (ml O_2/s)

$\dot{V}_{O_2 total}$ — $\dot{V}_{O_2}$ from 30 s before onset of first dive in bout until return to RMR after last dive in bout (ml O_2/s)

W_{stroke} — work of stroking during descent and bottom phases for respective dive type (ml O_2) $= (MR_{total} \times t_{dive}) - (RMR \times t_{asc})$

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