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Effects of Air and Water Temperatures on Resting Metabolism of Auklets and Other Diving Birds

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ABSTRACT

For small aquatic endotherms, heat loss while floating on water can be a dominant energy cost, and requires accurate estimation in energetics models for different species. We measured resting metabolic rate (RMR) in air and on water for a small diving bird, the Cassin's auklet (*Ptychoramphus aleuticus*), and compared these results to published data for other diving birds of diverse taxa and sizes. For 8 Cassin's auklets (~165 g), the lower critical temperature was higher on water (21°C) than in air (16°C). Lowest values of RMR ($W\ kg^{-1}$) averaged 19% higher on water (12.14 ± 3.14 SD) than in air (10.22 ± 1.43). At lower temperatures, RMR averaged 25% higher on water than in air, increasing with similar slope. RMR was higher on water than in air for alcids, cormorants, and small penguins but not for diving ducks, which appear exceptionally resistant to heat loss in water. Changes in RMR (W) with body mass either in air or on water were mostly linear over the 5- to 20-fold body mass ranges of alcids, diving ducks, and penguins, while cormorants showed no relationship of RMR with mass. The often large energetic effects of time spent floating on water can differ substantially among major taxa of diving birds, so that relevant estimates are critical to understanding their patterns of daily energy use.

Introduction

Marine endotherms (birds and mammals) face unique thermal challenges in aquatic environments. Thermal conductivity is 23 times higher and specific heat four times higher in water than in air (White 1984). Moreover, as body size decreases, we expect

even greater mass-specific heat loss for small diving birds (de Vries and van Eerden 1995). Yet, diving birds weighing <2 kg are very abundant in polar and subpolar seas, where air and water are often below the birds' lower critical temperatures. Accordingly, diving birds can have very high food requirements (up to 67% of body mass per day for Cassin's auklet, *Ptychoramphus aleuticus*; Hodum et al. 1998), which may restrict them to areas of high food availability (Grémillet et al. 1999).

To assess the energy requirements of free-ranging birds, daily energy expenditure (DEE) is often estimated from laboratory and field measurements. A common approach is to construct time-energy budgets in which the durations of daily activities (e.g., resting, preening, swimming, diving, flying) are multiplied by their respective costs and summed (Grémillet et al. 2003). Many studies focus on activities with high cost, such as swimming or flying, but these activities can occupy a relatively small fraction of a diel period. In contrast, during periods at sea, a marine bird can spend 40%–80% of its time floating on the water surface (Falk et al. 2000; Systad et al. 2000; Yoda et al. 2001; Tremblay et al. 2003, 2005), so that for some species resting costs are a large portion of DEE (40%–60%; Walsberg 1983). Resting metabolic rate (RMR), which includes both basal metabolic rate (BMR) and thermoregulation costs at the ambient temperature, is thus a critical variable.

For example, Lovvorn et al. (2009) used a spatially explicit model to simulate the energy balance of spectacled eiders (*Somateria fischeri*) wintering in the Bering Sea. The costs of diving and flying, because they occupied only a small fraction of the day, were a relatively minor part of the overall energy budget, while nonforaging activities had by far the greatest total cost. Respirometry studies on captive birds suggested that the cost of surface swimming and resting on water at $-1.7^{\circ}C$ was about 50% higher than for resting on the ice in air at $-14^{\circ}C$. The ability of spectacled eiders to get out of the water and onto the ice to reduce their resting costs during nonforaging periods appeared critical to total costs for a 24-h cycle.

Because directly measuring the costs of different activities is expensive and time-consuming, multiples of BMR predicted from allometric relationships are often used; however, they may be problematic (Ellis 1984; Ellis and Gabrielsen 2002). When multiples of BMR for different activities are not based on measured values for a given species, but rather are predicted from allometric equations derived over a broad range of body masses and taxa, energy budgets may appreciably overestimate or underestimate DEE. For example, conventional extrapolations of BMR for northern gannets (*Morus bassanus*) underestimated fish consumption by >300%, mainly due to underestimation of thermoregulation costs (Montevecchi et al. 1984, 1988; Birt-Friesen et al. 1989).

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While allometry provides a simple and easy approach to predicting energy requirements from body mass, such equations for birds have shown great heterogeneity in the scaling exponent and intercept (White et al. 2007b). To address this problem, one or several variables known to affect metabolism have been included, such as environmental factors (air temperature, wind, precipitation; White et al. 2007a), phylogeny (passerine vs. nonpasserine; Lasiewski and Dawson 1967), circadian rhythm (active vs. resting phases; Aschoff and Pohl 1970; Aschoff 1981), or latitude (Ellis and Gabrielsen 2002; McKechnie et al. 2006). However, all these relationships are based on BMR, or the minimum energy expenditure for a bird in air at thermoneutral temperatures. Metabolic rates of seabirds often differ markedly from those estimated by standard equations (Ellis 1984; Bennett and Harvey 1987; Ellis and Gabrielsen 2002), and direct measurements of basal metabolism for seabirds are usually higher than predicted by Lasiewski and Dawson (1967) or Aschoff and Pohl (1970; Gabrielsen et al. 1988; Croll and McLaren 1993). These discrepancies may reflect the fact that many seabirds spend most of their lives at sea on cold water, where the temperature is well below their thermoneutral temperatures. For aquatic birds, costs of thermoregulation while floating on water at different temperatures are especially important for accurate estimates of energy requirements.

Thermal conductance, defined as heat flow rate per unit surface area per unit temperature difference from an animal's core to its environment (Gates 1980), also scales allometrically with body mass (Herreid and Kessel 1967; Aschoff 1981; Gavrilov and Dolnik 1985; de Vries and van Eerden 1995; Schleucher and Withers 2001; Ellis and Gabrielsen 2002). However, empirical models of thermal conductance have been constructed mostly from heating or cooling rates of carcasses (Herreid and Kessel 1967; de Vries and van Eerden 1995; Luna-Jorquera et al. 1997), which does not account for alteration of heat flow at the body surface by changes in posture, vasomotion, piloerection, or evaporation of water. In addition, only a few studies have measured conductance of living animals while floating on water (Stahel and Nicol 1982; Jenssen and Ekker 1989, 1991; Jenssen et al. 1989; Croll and McLaren 1993). For these reasons, we limit this article to resting metabolism.

Lower critical temperature (T_{LC}), or the environmental temperature below which an endotherm must expend energy to thermoregulate, is often higher on water than in air (e.g., Prange and Schmidt-Nielsen 1970; Gabrielsen et al. 1988). Moreover, the rate of increase in metabolic rate as ambient temperature decreases below T_{LC} is often steeper on water. For example, in the little penguin (*Eudyptula minor*, body mass ~ 1 kg), the metabolic rate while resting on water ($RMR_{\text{water}} = 7.90 \text{ W kg}^{-1}$) was 60% higher than for resting in air ($RMR_{\text{air}} = 4.93 \text{ W kg}^{-1}$) at 15°C , but 178% higher at 5°C ($RMR_{\text{water}} = 16.27 \text{ W kg}^{-1}$, $RMR_{\text{air}} = 5.86 \text{ W kg}^{-1}$; Stahel and Nicol 1982). Activity metabolic rates (AMR; Bennett and Harvey 1987) or DEE (Walsberg 1983; Goldstein 1988) for birds measured by different methods (respirometry, doubly labeled water, food consumption) have much shallower slopes (logarithmic exponents) relative to body mass M_b ($M_b^{0.55}$ to $M_b^{0.61}$) than traditional allo-

metric equations of BMR ($M_b^{0.7}$). This difference implies that multiples of BMR are not consistent across body sizes. For birds living on water, greater surface area and presumably greater heat loss to water of small birds may result in even greater multiples of BMR with decreasing water temperatures. The metabolic response to being in water may also differ among major taxa; for example, cormorants with wettable plumage have much higher metabolic rates in water than do penguins of similar size (Schmid et al. 1995; Enstipp et al. 2005). In summary, if differences in RMR between air and water increase with decreasing water temperature and these patterns vary among taxa or with body size, constant multiples of BMR may not accurately represent the elevation in metabolism with decreasing ambient temperature.

To gain further insight into patterns of elevated metabolic rate for birds floating on water versus resting in air at varying temperatures, we measured the RMR of a small diving bird, the Cassin's auklet (*Ptychoramphus aleuticus*), in the family Alcidae. Because these auklets are small (<200 g) they presumably have high mass-specific heat loss to water and high costs of thermoregulation. Nevertheless, Cassin's auklets inhabit a wide latitudinal range of water temperatures, from Alaska (4°C) to Baja, Mexico (20°C). We also compared our results for Cassin's auklets with published data on RMR for four groups of diving birds (alcids, diving ducks, cormorants, penguins) while resting in air and on water at a range of ambient temperatures. Important questions were: (1) how do air and water temperatures affect the resting metabolic rate of a small diving bird, and (2) can we estimate the relative costs of resting in air and on water at various temperatures for species of differing body size and taxonomic group? In comparing data for different species, we found large variations that appeared to result from differences in experimental conditions or behavioral state of the birds. When apparent, we alert the reader to these sources of variation.

Material and Methods

Care of Captive Auklets

Eight captive-raised Cassin's auklets collected as chicks (20–30 d old) on Triangle Island, British Columbia, in 2005 were housed indoors at the University of Wyoming, Laramie. Birds were kept in a net-covered fiberglass tank (1.2 m \times 4 m \times 1 m) with continuously flowing fresh water (nonchlorinated, artesian well) 40 cm deep ($10^\circ\text{--}15^\circ\text{C}$). Air temperature in the auklet room was maintained at $<20^\circ\text{C}$, and full-spectrum overhead lighting was varied with the local photoperiod of Vancouver, British Columbia. Twice daily, auklets were fed thawed Antarctic krill (*Euphausia superba*) and 1-cm pieces of market squid (*Loligo opalescens*; tentacles, ink sac, and pen removed), and filleted mackerel (*Scomber scombrus japonicus*) mixed with vitamins (thiamin E paste, Mazuri Test Diet, St. Louis). To encourage regular diving and feeding underwater, a ball of frozen krill was hung in the water column of the tank daily. Auklets were at least 2 years old before the start of experiments, and

all experiments complied with animal care and use requirements of the University of Wyoming (A-3216-01).

Respirometry of Auklets

Open-flow respirometry was used to measure the RMR of auklets resting in air or floating on water at a range of temperatures. Air temperature inside and outside the chamber and water temperature at a depth of 10 cm were measured with thermocouples. These temperatures, air flow rate, and concentrations of O₂ and CO₂ were monitored continuously with a FoxBox and ExpeData software (Sable Systems, Las Vegas, NV). Before experiments, auklets were fasted >5 h and considered postabsorptive (Hilton et al. 2000; Richman and Lovvorn 2003, 2004). Measurements were made during the active phase (0900–1600 hours) of the diurnal cycle in darkened respirometry chambers.

For metabolic measurements in air, we used cylindrical plexiglass chambers (diameter, 40 cm; height, 12 cm; volume, 25 L). Respirometry chambers were placed in temperature-controlled cabinets (Frigidaire, Martinez, GA) maintained at air temperatures (T_a) between -10° and 30°C . For measurements in water, birds were acclimated to experimental conditions for at least 2 wk in a small fiberglass tank (1 m³) with water depth of ~ 25 cm. Water temperature (T_w) was varied by adding ice or warm tap water, and birds were allowed to rest at each T_w for >1 h before measurements. A plexiglass pyramidal chamber (base length, 47 cm; height, 44 cm; volume 36 L) was lowered over the birds to 4 cm below the water surface to form a tight seal. Air entered and exited the chamber 30 cm and 15 cm above the water surface, respectively, and was equilibrated to $\pm 4^\circ\text{C}$ of T_w .

Air was drawn through the chambers at $4.3\text{--}5.2\text{ L min}^{-1}$ by a vacuum pump monitored with a mass flowmeter (GFM 37, Aalborg Instruments, Orangeburg, NY), and dried with Drierite before being subsampled by the FoxBox at 150 mL min^{-1} to measure O₂ and CO₂ concentrations in air exiting the chamber. Each week the entire system was tested for leaks by the nitrogen dilution technique (Fedak et al. 1981), and O₂ and CO₂ concentrations of ambient air (20.95% and 0.04%, respectively) were calibrated before and after each experimental run by drift correction in ExpeData. Rates of O₂ consumption (\dot{V}_{O_2} , mL O₂ s⁻¹) and of CO₂ production (\dot{V}_{CO_2} , mL CO₂ s⁻¹), corrected for STP, were calculated by the fractional equivalent method of Withers (1977) and Bartholomew et al. (1981) outlined in Richman and Lovvorn (2008). For each bird on each experimental day, the respiratory quotient (RQ) was calculated as the ratio of \dot{V}_{CO_2} to \dot{V}_{O_2} . We calculated mass-specific energy cost (W kg⁻¹) from the rate of oxygen consumption (\dot{V}_{O_2}) using the RQ measured for each experimental bird on each experimental day. We used energy equivalents of $19.8\text{ J (mL O}_2\text{)}^{-1}$ and $20.1\text{ J (mL O}_2\text{)}^{-1}$ for RQs of 0.7 and 0.8, respectively.

RMRs in air and while floating on water were plotted for all temperatures measured. To determine the lower critical temperature (T_{LC}), we removed measurements of heat-stressed individuals above 25°C and used a continuous two-phase,

straight-line regression procedure following the methods of Nickerson et al. (1989). In brief, the data were divided into two phases (from 5° to 20°C in air and 5° to 22°C on water at 1°C increments), and we used least squares regression to determine the slope and intercept of each phase with a continuity restriction that joined the two lines. We sequentially fitted the two phases until the combined sum of squared error (SSE) was minimized. Because the slope in phase 2 did not differ significantly from 0 for the candidate models, we repeated the procedure with phase 2 as a horizontal line and tested whether the reduced model differed significantly from the complete model, using an *F*-test (see eq. [15] of Nickerson et al. 1989). T_{LC} was calculated as the point where the lines representing elevated metabolism at low ambient temperature (either T_a or T_w) intersected the line representing RMR within the thermoneutral zone in air, or the range of temperatures of minimum metabolic rate on water.

Any auklet that was agitated or exceptionally active during the experiment was removed from the chamber, and only measurements of birds resting quietly or floating with minimal swimming were used in analyses. Because some individuals were highly active, especially at cold temperatures, not all birds were measured at every temperature. Each bird was weighed at the beginning and end of an experimental run.

RMR of Diving Birds in Air and Water

In our literature review, we were concerned not with basal metabolism (BMR) but rather with resting metabolism (RMR) for species at varying temperatures in air and floating on water. RMR includes both BMR and thermoregulation costs. We limited our review to avian divers for which there were sufficient numbers of measurements for animals resting on water. As with any compilation of data from the literature, data quality was highly variable. Principal shortcomings were inadequate measurements of air or water temperature or lack of data on body mass. Where necessary, values of temperature or body mass were obtained from published studies on the same species using the same experimental protocol or apparatus. We included measurements in air and on water for four families of avian divers: Alcidae (auks and puffins), Anatidae (diving ducks), Phalacrocoracidae (cormorants), and Spheniscidae (penguins). Although there are a number of RMR measurements for Procellariidae in air (review in Ellis and Gabrielsen 2002), for this group we are aware of no measurements for resting on water that adhere to our selection criteria (see next section).

Selection Criteria

For each species, we included metabolic measurements if they met the following criteria: (i) Measurements were on adults. (Measurements for sub-adults include elevated metabolism due to growth and were excluded.) (ii) Measurements were as oxygen consumption by open-flow respirometry. (Measurements based on CO₂ production or closed-circuit respirometry were excluded to eliminate differences among methods.) (iii) Mea-

measurements were made on postabsorptive individuals starved <15 h. Long-term fasts observed in taxa such as penguins and eiders can affect metabolic rate as well as RQ, due to changes in relative amounts of lipid or protein catabolized (Le Maho et al. 1981; Cherel et al. 1988). (iv) Measurements were made on unrestrained birds under metabolic chambers while floating on water. (Birds that are restrained or wearing metabolic masks are likely to have elevated metabolism.) (v) Measurements were made between -15° and 40°C in air, and between 0° and 30°C on water.

It is often difficult to discern a difference in metabolism between active and resting phases of many high-latitude seabirds (Ricklefs and Matthew 1983; Brown and Adams 1984; Baudinette et al. 1986; Gabrielsen et al. 1988), and the time of day that measurements were taken was not always reported. Thus, we included metabolic measurements regardless of time of day. Although measurements with low sample size are more prone to error, we accepted low sample sizes for species that are difficult to obtain or keep in captivity. To maintain rigorous methodological standards for comparisons among studies and to ensure that an international readership could access the same data sources, we used data only from peer-reviewed publications. For these same reasons, data from unpublished studies that were tabulated in publications by others were also excluded.

Data obtained from the literature were converted from published values of oxygen consumption to units of energy (J). This conversion can be confounded by differences in the caloric equivalent (Ellis and Gabrielsen 2002). Often a caloric equivalent of $20.08 \text{ kJ (L O}_2\text{)}^{-1}$, representing an RQ of 0.79 or higher, is used to convert oxygen consumption to energy. Because the diets of diving birds generally have high lipid and limited carbohydrate content, an RQ of <0.79 (caloric equivalent of $19.8 \text{ kJ [L O}_2\text{]}^{-1}$) is more reasonable. High RQs sometimes reported for seabirds are difficult to explain; for example, the RQ = 0.9 for South Georgian shag = imperial cormorant *Phalacrocorax atriceps* (Bevan et al. 1997) suggests a diet of up to 40% carbohydrate in a carnivore. In this article, we have used the RQ value reported in the original publication, if it was measured, or else have assumed 0.7. Rate of oxygen consumption was converted to SI units using an energy equivalent of $19.8 \text{ J (mL O}_2\text{)}^{-1}$ for $\text{RQ} \leq 0.79$ and $20.1 \text{ J (mL O}_2\text{)}^{-1}$ for $\text{RQ} \geq 0.80$.

For each of the avian divers examined, we plotted RMR versus temperature of air or water. Based on all measurements of resting metabolism at varying temperatures, we also plotted RMR in air and on water as a function of body mass on an arithmetic scale for the alcids, diving ducks, cormorants, and penguins. Plots of BMR versus body mass M_b are often expressed allometrically, that is, by fitting a straight line by least squares regression to log-transformed data and back transforming that equation to an exponential function (Calder 1974; Peters 1983). However, log transformation can conceal influential outliers, and one must use arithmetic and not logarithmic values when applying the results (Packard and Boardman 2008, 2009). Thus, we have plotted RMR versus M_b on an arithmetic scale.

Results

RMR of Auklets in Air and Water

For 8 Cassin's auklets (mean mass = $165 \text{ g} \pm 17 \text{ SD}$), we determined RMR in air and on water using a continuous two-phase, straight-line regression procedure following the methods of Nickerson et al. (1989). For the complete model with the lowest SSE, the slope of phase 2 (representing RMR) did not differ significantly from 0 ($P = 0.224$ in air and $P = 0.104$ on water). We repeated the analysis with a reduced model with only the intercept parameter for phase 2 and found no significant difference between the complete and the reduced model (in air $F_{1,37} = 0.356$, $P = 0.55$; on water $F_{1,26} = 3.093$, $P = 0.09$). Lower critical temperature (T_{LC}) below which RMR (W kg^{-1}) rose above the minimum, was higher on water (21°C) than in air (16°C ; Fig. 1). The lowest values of RMR above the respective values of T_{LC} averaged 19% higher on water ($12.14 \pm 3.14 \text{ SD}$, $21^{\circ}\text{--}25^{\circ}\text{C}$) than in air ($10.22 \pm 1.43 \text{ SD}$, $16^{\circ}\text{--}25^{\circ}\text{C}$; t -test, $P = 0.10$). As temperature (T) decreased further, RMR was 25% higher on water than in air, increasing with similar slope on water as in air (on water at 0° to 21°C , $\text{RMR}_{\text{water}} = 19.67 - 0.36T_w$, $r^2 = 0.42$, $P < 0.001$; in air at -10° to 16°C , $\text{RMR}_{\text{air}} = 15.70 - 0.34T_a$, $r^2 = 0.58$, $P < 0.001$).

For Cassin's auklets, the upper critical temperatures (T_{UC}) were difficult to distinguish between air and water because the

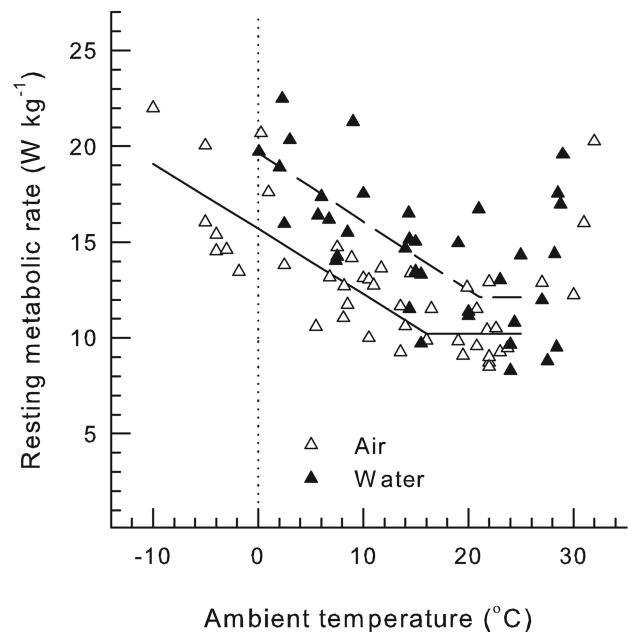


Figure 1. Resting metabolic rate (RMR; W kg^{-1}) for adult, captive, postabsorptive Cassin's auklets (mean mass = $165 \text{ g} \pm 17 \text{ SD}$, $n = 8$) resting in air (RMR_{air}) or floating on water ($\text{RMR}_{\text{water}}$) at varying temperatures ($^{\circ}\text{C}$). In air, RMR between 16°C and 25°C was $10.22 \text{ W kg}^{-1} \pm 1.43 \text{ SD}$ with lower critical temperature $T_{LC\text{air}} = 16^{\circ}\text{C}$, and RMR below 16°C was described by $\text{RMR}_{\text{air}} = 15.70 - 0.34T_a$ ($r^2 = 0.58$, $P < 0.001$). In water, RMR between 21° and 25°C was $12.14 \text{ W kg}^{-1} \pm 3.14 \text{ SD}$ ($T_{LC\text{water}} = 21^{\circ}\text{C}$), and RMR below 21°C was described as $\text{RMR}_{\text{water}} = 19.67 - 0.36T_w$ ($r^2 = 0.42$, $P < 0.001$).

Table 1: Resting metabolic rate in air (RMR_{air}) and mean body mass for alcids, diving ducks, cormorants, and penguins measured by open-flow respirometry on postabsorptive adults

Species	n	Mass \pm SD (kg)	$RMR_{air} \pm$ SD (W kg ⁻¹)	T_a obs (°C)	T_{LCair} (°C)	RQ	Regression for $RMR_{air} < T_{LC}$	Reference
Alcids:								
Common murre (<i>Uria aalge</i>)	4	.771 \pm .061	5.85 \pm .55	9		.75		Bryant and Furness 1995
	8	.836 \pm .076	7.18	20		.8		Croll and McLaren 1993
Thick-billed murre (<i>Uria lomvia</i>)	11	.819 \pm .073	6.13 \pm .66	>2	2	.72	6.29--.17 T_a	Gabrielsen et al. 1988
	5	.82 \pm .07	6.68 \pm .51	7		.71		Hawkins et al. 1997
	6	.803 \pm .050	8.60	20		.8		Croll and McLaren 1993
Razorbill (<i>Alca torda</i>)	2	.589 \pm .031	6.07 \pm .83	10		.77		Bryant and Furness 1995
Black guillemot (<i>Cepphus grylle</i>)	13	.342 \pm .022	8.78 \pm .66	>7	7	.72	10.65--.22 T_a	Gabrielsen et al. 1988
Atlantic puffin (<i>Fratercula arctica</i>)	4	.329 \pm .018	7.73 \pm 1.05	9		.78		Bryant and Furness 1995
Cassin's auklet (<i>Ptychoramphus</i> <i>aleuticus</i>)	8	.165 \pm .017	10.22 \pm 1.43	>16	16	.7	15.70--.34 T_a	This study
Dovekie (<i>Alle alle</i>)	16	.152 \pm .012	13.36 \pm .72	>5	4.5	.75	14.54--.26 T_a	Gabrielsen et al. 1991b
Least auklet (<i>Aethia pusilla</i>)	5	.083	16.01 \pm 1.17	15		.8		Roby and Ricklefs 1986
			20.00 ^c	10				
Diving ducks:								
Common eider (<i>Somateria mollissima</i>)	12	1.661 \pm .251	4.75 \pm .39 ^s	>7	7	.7	5.81--.14 T_a	Gabrielsen et al. 1991a
	6	1.790 \pm .130	4.22 \pm .35	>2	2	.77		Hawkins et al. 2000
	7	1.660 \pm .170	3.68 \pm .48 ^w	>1.5	1.5	.71	3.46--.07 T_a	Jenssen et al. 1989
Long-tailed duck (<i>Clangula hyemalis</i>)	5	.490 \pm .026	5.60 \pm .32 ^w	>18	18	.71	9.06--.19 T_a	Jenssen and Ekker 1989
New Zealand scaup (<i>Aythya</i> <i>novaezelandiae</i>)	2	.488	4.80	16--33	16	.8		McNab 2003
Cormorants:								
Blue-eyed shag (<i>Phalacrocorax atriceps</i>)	6	2.63 \pm .24	6.60 \pm 1.32	20	0	.71		Chappell et al. 1989
South Georgian shag (<i>Phalacrocorax</i> <i>atriceps georgianus</i>)	3	2.39 \pm .16	5.81 \pm .31	8.4		.9		Bevan et al. 1997
Great cormorant (<i>Phalacrocorax carbo</i>)	5	2.56 \pm .43	3.10 \pm .34	20		.8		Schmid et al. 1995
Double-crested cormorant (<i>Phalacrocorax auritus</i>)	10	2.10 \pm .16	4.59 \pm .51	22.1		.71	7.22--.13 T_a (6.2°--25.4°C)	Enstipp et al. 2006

Table 2: Resting metabolic rate while floating on water (RMR_{water}) and mean body mass for alcids, ducks, cormorants, and penguins measured by open-flow respirometry on postabsorptive adults

Species	n	Mass \pm SD (kg)	$RMR_{water} \pm$ SD ($W \text{ kg}^{-1}$)	T_w obs ($^{\circ}C$)	$T_{LC,water}$ ($^{\circ}C$)	RQ	Regression for $RMR_{water} < T_{LC}$	Reference
Alcids:								
Common murre (<i>Uria aalge</i>)	8	.836 \pm .076	7.30	>15	15	.8	17.39–.60 T_w	Croll and McLaren 1993
Thick-billed murre (<i>Uria lomvia</i>)	6	.803 \pm .050	8.84	>16	16	.8	20.99–.77 T_w	Croll and McLaren 1993
Cassin's auklet (<i>Pychoramphus aaleuticus</i>)	8	.165 \pm .017	12.14 \pm 3.14	21–25	21	.7	19.67–.36 T_w	This study
Diving ducks:								
Common eider (<i>Somateria mollissima</i>)	7	1.791 \pm .13	10.10 \pm 2.27 ^c	13.7–19		.77		Hawkins et al. 2000
	10	1.80 \pm .09	4.3 \pm .3	5.6		.85		Jenssen and Ekker 1991
	5	1.95 \pm .09	3.83 \pm .24 ^w	16–25	16	.71	5.48–.09 T_w	Jenssen et al. 1989
White-winged scoter (<i>Melanitta fusca</i>)	5	1.092	5.91	9		.8		Richman and Lovvorn 2008
Long-tailed duck (<i>Clangula hyemalis</i>)	5	.490 \pm .026	5.59 \pm .56	>12	12	.7	11.87–.50 T_w	Jenssen and Ekker 1989
Lesser scaup (<i>Aythya affinis</i>)	6	.591 \pm .073	7.94 \pm .66	13		.7 ^a		Stephenson 1994
	8	.536 \pm .054	5.02 \pm 1.47	23		.7		Kaseloo and Lovvorn 2005
	8	.553 \pm .122	7.70 \pm 1.95	8				
	8	.569 \pm .074	6.06 \pm 3.03	18		.76		Kaseloo and Lovvorn 2006
Tufted duck (<i>Aythya fuligula</i>)	6	.578 \pm .061	6.09 \pm 1.62 ^s	22.9		.86		Bevan and Butler 1992
	6	.605 \pm .027	10.90 \pm 1.60 ^w	7.4		.75		
	7	.571 \pm .037	7.56 \pm 2.77	14.4		.7 ^a		Bevan et al. 1992
	8	.6	5.83	22		.8	9.80–.18 T_w	de Leeuw 1996
	8	.6	8.33	8		.8		
	6	.613 \pm .066	5.51 \pm .88 ^c	17.8		.9		Woakes and Butler 1983
	6	.597 \pm .064	5.49 \pm .49 ^c	13.6		.84		Woakes and Butler 1983
	6	.725 \pm .066	6.93 \pm .68	15–18.5		.81		Halsey et al. 2003
Cormorants:								
Great cormorant (<i>Phalacrocorax carbo</i>)	16	2.56 \pm .43	14.1 \pm 1.12	12.6		.7		Schmid et al. 1995
South Georgian shag (<i>Phalacrocorax georgianus</i>)	3	2.39 \pm .16	9.02 \pm .29	6.9		.71		Bevan et al. 1997

Double-crested cormorant (<i>Phalacrocorax auritus</i>)	8	2.10 ± .16	10.83 ± 1.75	15	.71	Enstipp et al. 2006
	8	2.10 ± .16	14.62 ± 2.23	7.9	.71	19.48–.58T _w (8–16°C)
Brandt's cormorant (<i>Phalacrocorax penicillatus</i>)	3	2.0 ± .3	10.73 ± 1.22 ^d	19–21	.7	Ancl et al. 2000
	3	2.0 ± .3	6.67 ± 1.19 ⁿ	19–21	.7	
European shag (<i>Phalacrocorax aristotelis</i>)	3	1.67 ± .28	19.37 ± .73	5–13	.72	Enstipp et al. 2005
Penguins:						
Emperor penguin (<i>Aptenodytes forsteri</i>)	3	22 ^c	3.47	1.5–6	.7 ^a	Kooyman and Ponganis 1994
King penguin (<i>Aptenodytes patagonicus</i>)	8	11.5 ± 1.1	4.65 ± .48	9.1	.74	Culik et al. 1996
	10	10.93 ± .58	5.05 ± 1.11	8.9	.7	Fahlman et al. 2005
	6	10.3 ± .24	3.89 ± 1.31	8.9 ^a	.7	Halsey et al. 2007
Gentoo penguin (<i>Pygoscelis papua</i>)	5	4.8 ± .3	8.19	4	.68	Culik et al. 1991
Adélie penguin (<i>Pygoscelis adeliae</i>)	5	4.2 ± .3	8.36 ± 1.10	4	.68	Culik and Wilson 1991 Culik et al. 1991
Chinstrap penguin (<i>Pygoscelis antarctica</i>)	4	3.95 ± .40	8.75 ± .92	4	.68	Culik et al. 1991
Humboldt penguin (<i>Pygoscelis humboldtii</i>)	3	4.6 ± .2	4.27 ± .17	18	.63	Butler and Woakes 1984
	2	3.78 ± .09	7.2 ± 1.3 ^c	19.2	.7 ^a	Hui 1988
	3	3.60 ± .22	5.99 ± .67	19	.78	Luna-Jorquera and Culik 2000
Little penguin (<i>Eudyptula minor</i>)	12	1.2 ± .09	8.5	10	.7 ^a	Bethge et al. 1997
	4	1.2	6.40 ± .94	19–22		Baudinette and Gill 1985
	6	1.0 ± .08	9.24	10 ^a	.74	23.72–1.49T _w (<10 °C); 10.30–.16T _w (>10 °C) Stahel and Nicol 1982

Note. Conventions as in Table 1.

^aAssumed.

^bd = daytime, n = nighttime, s = summer, w = winter, c = control.

^cRegression or value was extrapolated from data provided.

data for water were so variable, but T_{UC} appeared to be about 25°C both in air and on water (Fig. 1). High variability of RMR on water may result partly from differences in posture while floating—some birds slept with their head tucked under a wing and one leg pulled into the plumage, while others floated with head erect and both legs extended, and they occasionally paddled.

RMR of Major Groups of Diving Birds

We plotted RMR in air and for floating on water at varying temperatures of six species for which data were available (Tables 1, 2; Fig. 2). Differences in experimental setup, behavioral state of the birds, and body masses of different species prevent detailed comparisons among studies, but some overall trends were apparent. RMR was substantially higher on water than in air at all temperatures for all species except the sea ducks, which showed little difference at temperatures >10°C. At lower temperatures on water, the rate of increase in RMR as temperature decreased was also less in the sea ducks than in the other species. For common eider (*Somateria mollissima*), there was in fact no clear T_{LC} either in air or on water; and on water, RMR showed relatively little increase with decreasing temperature compared to the RMR of the other species. The challenge of comparing data from different studies is emphasized by the very high value for resting on water at 14°C for common eider reported by Hawkins et al. (2000), which may reflect lack of behavioral acclimation to experimental conditions. Nevertheless, the overall impression is that compared to the other species, the sea ducks are unusual in experiencing little or no increase in heat loss to water versus air at temperatures above 10°C and much less rapid increase of heat loss to water with decreasing temperature. These patterns hold even when comparing long-tailed duck (*Clangula hyemalis*) to an alcid and a penguin of similar body mass (Fig. 2). Some of the lower sensitivity of common eider to temperature probably results from their large body mass. However, double-crested cormorants (*Phalacrocorax auritus*) of even larger mass responded as strongly to temperature change as the much smaller thick-billed murre (*Uria lomvia*) and little penguin, suggesting higher mass-specific sensitivity to temperature in cormorants both in air and on water.

RMR among Species of Ducks and Alcids

To explore variations among species within taxonomic groups, we plotted available data for alcids and diving ducks in air and floating on water at a range of temperatures (Fig. 3). Because publications often provided only regression equations and not data points, we present only fitted lines for the different species. Overall, the data are consistent in showing higher RMR ($W\text{ kg}^{-1}$) in both air and water as body mass decreases. In air, the increase in RMR as temperature decreases is often more rapid in smaller group members, but in water this trend is not consistent. Again, sea ducks (long-tailed duck, common eider) differ from alcids in losing little more heat to water versus to air

at temperatures >10°C and by their heat loss to water increasing at a much lower rate as water temperature declines.

RMR versus Body Mass

To explore variations among taxonomic groups, we plotted all available data (Tables 1, 2) for alcids, diving ducks, cormorants, and penguins of RMR (W) in air and floating on water in relation to body mass (Fig. 4). For eight alcid species over a range of temperatures in air, RMR (W) appears to scale almost linearly with body mass (Fig. 4A; Table 3). Due to a limited number of measurements, we did not fit a curve for alcids floating on water. Similar to the alcids, the diving ducks (Fig. 4B) show linear increase in RMR as a function of body mass both in air and on water, with higher values for water. The metabolic rate for common eider floating on water measured by Jenssen et al. (1989) at 16°C was 3.83 W kg^{-1} , 4% higher but not significantly different from RMR in air at $T_a > 1.5^\circ\text{C}$. Conversely, RMR for common eider measured by Hawkins et al. (2000) in water at similar temperatures (14°–19°C) was 10.10 W kg^{-1} , 139% higher than their own measurements in air at $T_a > 2^\circ\text{C}$ (4.22 W kg^{-1}), and 164% higher than RMR in air at 16°C reported by Jenssen et al. (1989). Because the value of Hawkins et al. (2000) for resting on water seems too high (Fig. 4B; see “Discussion”), it was excluded from the linear regression (Table 3).

For cormorants, there is no clear trend in RMR (W) with body mass either in air or on water (Fig. 4C; Table 3). The difference between values in air and on water is greater in cormorants than in the other groups, perhaps because of the cormorants' wettable plumage (Grémillet et al. 2005). For penguins (Fig. 4D), which span a much larger range of body mass (1–22 kg) than the other groups, increase in RMR with body mass appears to be mostly linear both in air and on water, with higher values on water.

RMR Difference in Air versus Water

For 13 species, we were able to compare the relative increase in metabolism for birds resting in air at apparent thermoneutral temperatures (RMR_{air} at TNZ) and while floating on water $\text{RMR}_{\text{water}}$ with decreasing temperatures (Table 4). In some cases, measurements of RMR_{air} at TNZ and $\text{RMR}_{\text{water}}$ were derived from the same study, while in other cases values were drawn from different studies. As expected, the magnitude of increase in $\text{RMR}_{\text{water}}$ relative to RMR_{air} at TNZ increased with decreasing water temperature; however, the amount of this increase was not consistent for all species. In particular, the cormorants appear to be the most sensitive to decreasing water temperatures, while the ducks appear least sensitive.

Discussion

In all groups except diving ducks, RMR was always substantially higher when floating on water than in air at the same temperature, and this difference increased with decreasing temperature (Fig. 2). Although the very small-bodied Cassin's auk-

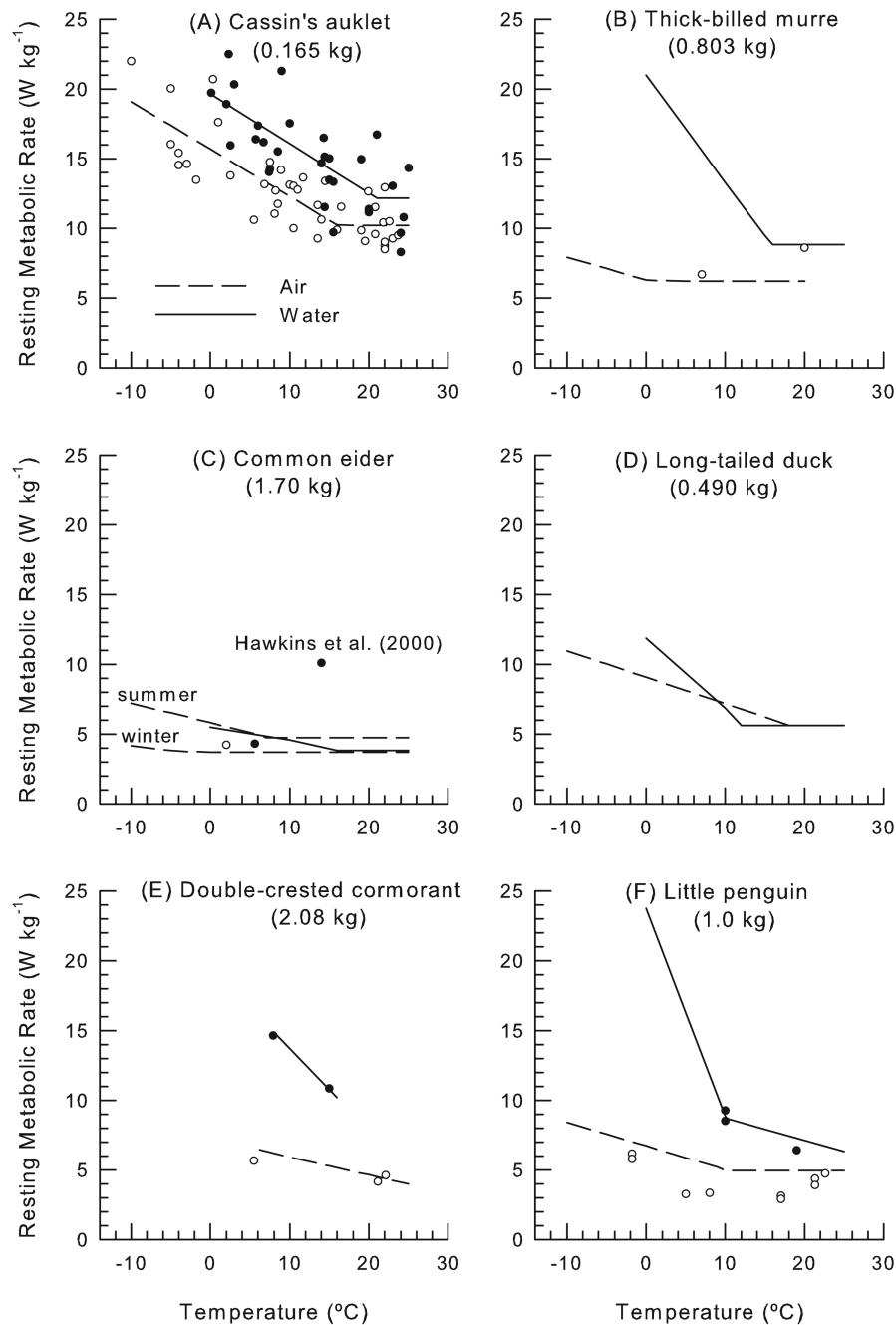


Figure 2. Resting metabolic rate in air and on water of six species for which data over a range of temperatures from single studies were available. A, Cassin's auklet (see Fig. 1); B, thick-billed murre; C, common eider; D, long-tailed duck; E, double-crested cormorant; and F, little penguin. Regression lines in air (dashed) or on water (solid) are provided where available. Measurements from different studies at single temperatures in air (open symbols) or on water (solid symbols) are also shown. Data are from Tables 1 and 2.

let did have higher RMR both in air and on water than the larger species, its small size did not result in more rapid rise in RMR with decreasing temperature; thick-billed murre, double-crested cormorant, and little penguin all showed greater rates of increase in RMR at cold temperatures than did Cassin's auklet. Despite its large size, the double-crested cormorant showed patterns of RMR similar to the smaller thick-billed

murre and little penguin (Fig. 2E vs. 2B, 2F). Although this response in water might result from the cormorants' wettable plumage (Grémillet et al. 2005), wettability does not explain the close similarity of cormorants to these smaller species in response to air temperature. Cormorants appear to have relatively higher heat loss than the other groups both in air and on water (cf. Hennemann 1983; Schmid et al. 1995).

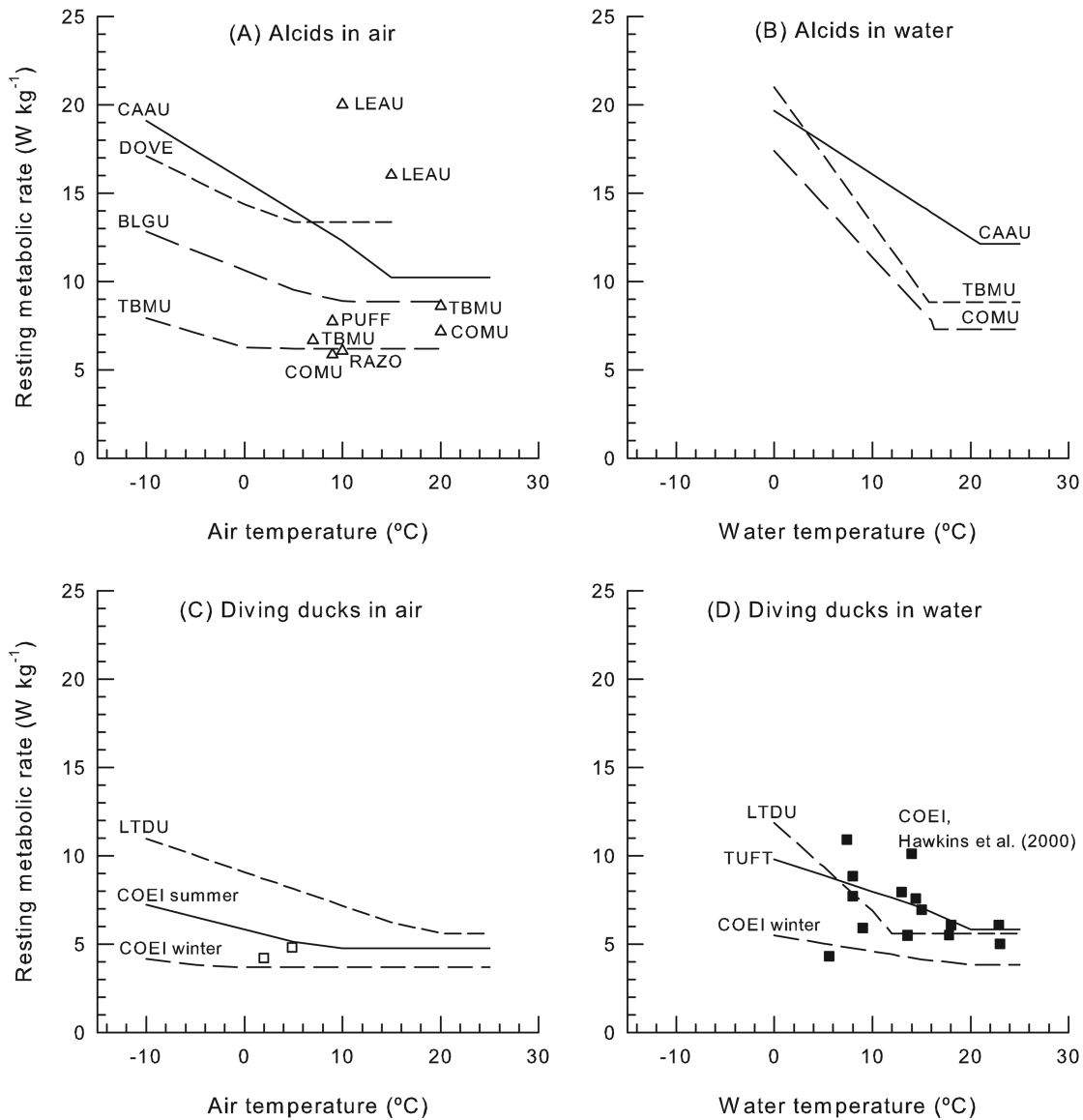


Figure 3. Resting metabolic rate for alcids and diving ducks in air and floating on water at varying temperatures. Regression lines for single studies in which data were collected over a range of temperatures are given in Tables 1 and 2 as are data points from different studies using only a single temperature. PUFF = Atlantic puffin, BLGU = black guillemot, TBMU = thick-billed murre, COMU = common murre, CAAU = Cassin's auklet, DOVE = dovekie, LEAU = least auklet, RAZO = razorbill, COEI = common eider, LTDU = long-tailed duck, and TUFT = tufted duck. Data are from Tables 1 and 2.

In contrast to the other taxonomic groups, the sea ducks showed little or no effect of being on water versus in air at temperatures above about 10°C, and below 10°C on water the increase in RMR with decreasing temperature was more gradual in ducks than in the other groups. Interestingly, grebes may show similar patterns to the ducks (Ellis and Jehl 2003). For the large-bodied common eider, there was in fact no clear T_{iC} in either medium, with no effect of temperature on RMR in air in summer-acclimatized birds, and no appreciable effect of being on water versus in air during winter at any temperature. Common eider and long-tailed duck are apparently

much more cold-adapted than either thick-billed murre or little penguin, whose geographic ranges extend to lower latitudes. Large sea ducks are more buoyant than other aquatic birds (Lovvorn and Jones 1991), probably because of their exceptionally thick plumage and associated insulative air layer. Although some great cormorants (*Phalacrocorax carbo*) do inhabit arctic waters, their exceptionally high capture rates allow them to spend minimal time in the water, and cormorants are believed to have evolved in much warmer environments than alcids, sea ducks, or penguins (Grémillet et al. 1999, 2004). Despite the confounding influence of differing

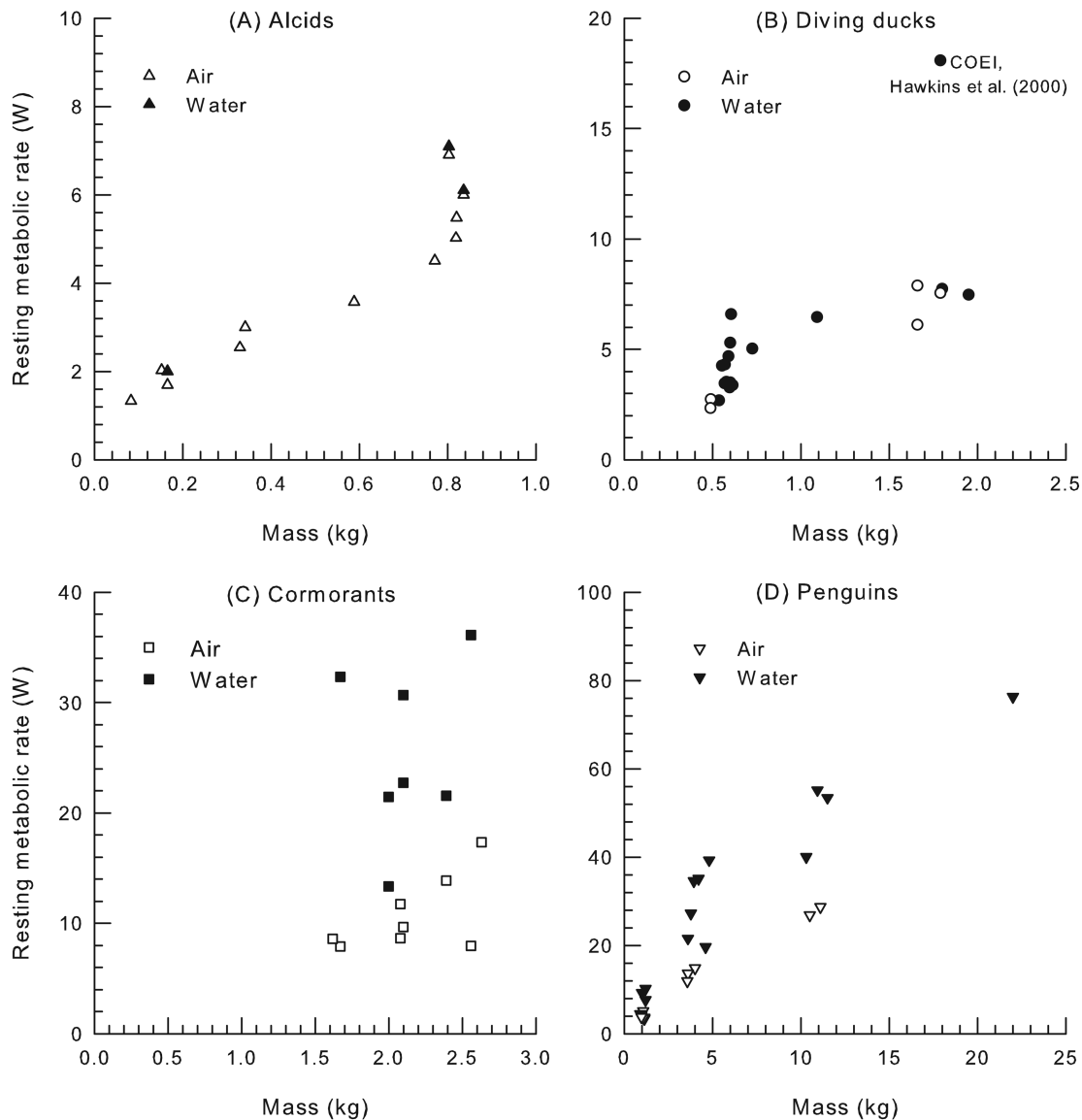


Figure 4. Resting metabolic rate (W) versus body mass in air and on water for alcids (A), diving ducks (B), cormorants (C), and penguins (D). Data are from Tables 1 and 2.

experimental conditions, our results show that the response of RMR to being in air versus on water, as well as response to changing temperature in either medium, differs greatly between major taxonomic groups of diving birds regardless of body size.

Within the groups of alcids and diving ducks, trends in effects of body size on the magnitude of RMR are generally consistent both in air and on water, with RMR ($W \text{ kg}^{-1}$) increasing with decreasing body size (Fig. 3). Although the greater heat loss in smaller than larger birds tended to increase as temperature decreased in air, that pattern did not persist in water. The tendency of alcids to lose more heat than diving ducks in water and for that loss to increase more rapidly as temperature decreases than in ducks, held true for all mem-

bers of these two groups. Based on comparisons between alcids and diving ducks, it appears that body size scaling of RMR may apply within but not between taxonomic groups and in air but not on water.

When body mass scaling of RMR (W) was examined only within major groups (Fig. 4), the relations were predictable and essentially linear for alcids in air, and for diving ducks and penguins both in air and on water (measurements for alcids in water were too few for analysis). The linearity held not only over the 5- to 10-fold range of body mass for diving ducks and alcids, but also over the 22-fold range of body mass for penguins. For diving ducks and penguins, slopes of the relationships were higher on water than in air (Table 3). For cormorants, there was no clear trend of body mass scaling of RMR

Table 3: Linear regressions of resting metabolic rate (RMR; W) in relation to body mass M_b (kg) in air and floating on water for different taxonomic groups of diving birds (see Fig. 4)

Group	Air				Water			
	a	b	r^2	P	a	b	r^2	P
Alcids	5.64	.92	.90	<.01				
Diving ducks	3.83	.67	.94	<.01	2.93 ^a	2.37 ^a	.64 ^a	<.01
Cormorants	5.53	-1.14	.37	.11	4.84	15.23	.03	.70
Penguins	2.46	2.11	.97	<.01	3.19	12.65	.86	<.01

Note. Regressions are for an arithmetic scale (not log transformed) in the form RMR_{air} or $RMR_{water} = aM_b + b$.

^aExcluding Hawkins et al. 2000.

either in air or on water, although values on water were higher than in air (Table 3; Fig. 4).

Variations among Studies

A major challenge in comparing RMR measurements among studies is the strong effect of different experimental conditions and behavioral state of the birds. Two examples will illustrate this point.

For thick-billed murre (mass ~ 0.8 kg), Croll and McLaren (1993) found no significant difference ($\sim 3\%$) between birds resting in air (8.60 W kg^{-1} at $20^\circ C$) and those floating on water (8.84 W kg^{-1} at $16^\circ C$) for the range of temperatures of minimal metabolic rate. However, other studies on thick-billed murre have reported much lower mass-specific metabolism at colder air temperatures. Gabrielsen et al. (1988) found RMR_{air} at $>2^\circ C$ of 6.13 W kg^{-1} , which is 29% lower than the RMR_{air} and 31% lower than the RMR_{water} reported by Croll and McLaren (1993). Moreover, the relative increase in metabolism while resting on water with decreasing temperature (T_w) for thick-billed murre (Fig. 2B) shows a much steeper slope than those of the smaller Cassin's auklet (Fig. 2A) and ducks of comparable size (Fig. 2D). This pattern might indicate that the larger murre are more sensitive to decreasing water temperatures than the smaller Cassin's auklet, but without measurements for other small alcids such a conclusion is tentative.

Metabolic measurements of common eider (mass ~ 1.7 kg) also vary greatly among studies. Jenssen et al. (1989) reported no significant difference between RMR_{air} at $T_a > 1.5^\circ C$ (3.68 W kg^{-1}) and RMR_{water} at T_w of 16 – $25^\circ C$ (3.83 W kg^{-1}). Similar measurements on nonincubating eiders during summer by Gabrielsen et al. (1991a) yielded RMR_{air} of 4.75 W kg^{-1} at thermoneutral temperatures ($T_{LCair} > 7^\circ C$), a value 29% higher than the value for air reported by Jenssen et al. (1989), and 24% higher than Gabrielsen et al.'s (1991a) value on water.

For common eider, Hawkins et al. (2000) reported RMR in air (4.22 W kg^{-1} , $T_{LCair} = 2^\circ C$) that was similar to that of Jenssen et al. (1989) in winter and Gabrielsen et al. (1991a) in summer. However, the RMR_{water} reported by Hawkins et al. (2000) of 10.10 W kg^{-1} at fairly warm water temperatures (14 –

$19^\circ C$) is quite high. This measurement is 139% higher than their own measurement in air and 164% higher than the RMR_{water} reported by Jenssen et al. (1989) at similar water temperatures. It is possible that the common eiders measured by Hawkins et al. (2000), in a swim flume with the motor off, were excited by the experimental conditions, resulting in very high metabolic rates while on water. We cannot judge whether the measurement of Hawkins et al. (2000) is too high or that of Jenssen et al. (1989) is too low, although Hawkins et al.'s value is conspicuous when placed in a comparative context (Figs. 2C, 3D, 4B).

Birds used in experiments often have unique temperaments both between species and among individuals of the same species. While some species settle down quickly under experimental conditions (e.g., lesser scaup, *Aythya affinis*; mallard, *Anas platyrhynchos*), other species take a long time to acclimate to metabolic chambers, if they acclimate at all (e.g., auklets, scoters, possibly eiders). Measurements presented in Figure 1 were collected only on auklets that appeared calm in the metabolic chamber, and we had to acclimate some of the birds for several weeks before they would settle down under the metabolic dome. The psychological state of the animals can have large effects on measurements of RMR either in air or on water.

Effects of Error in Measurement or Extrapolation

Effects of varying experimental conditions discussed in the previous section or of extrapolating values from inappropriate taxa can have important consequences for models of energy expenditure. As an example in constructing time-energy budgets, if a common eider floated on water at $15^\circ C$ for a conservative estimate of 17 h d^{-1} ($\sim 70\%$ of a 24-h period; see Systad et al. 2000), the total daily cost of that activity based on the values of Jenssen et al. (1989) would be ~ 457 kJ ($RMR_{water} = 3.83$ W $kg^{-1} = 26.89$ kJ h^{-1}). Conversely, if we used the RMR_{water} at similar water temperatures reported by Hawkins et al. (2000) ($RMR_{water} = 10.10$ W $kg^{-1} = 65.12$ kJ h^{-1}), the total cost would be $\sim 1,107$ kJ, nearly 2.5 times higher. Such an increase over 70% of the day could double the estimate of required food intake based on a value that appears much too high relative to other measurements (Figs. 2C, 3D, 4B). Similar discrepancies could result from extrapolating values for diving ducks to alcids, cormorants, or penguins, which show quite different responses to being in water at different temperatures (Figs. 2–4).

Ecological Importance of RMR on Water

During long periods of resting, the effect of water temperature on energy costs is even greater than during active foraging (Enstipp et al. 2006). During foraging and other activities, heat generated by muscular work or by digestion (specific dynamic effect) can be used to substitute for thermogenesis. Exercising muscles are seldom $>25\%$ efficient, resulting in production of exercise heat. However, this "waste" heat can reduce the need to generate heat by shivering, substantially reducing the cost of thermoregulation (review in Lovvorn 2007). When nondi-

Table 4: Comparison of resting metabolic rates in air at thermoneutral temperatures (RMR_{air} at TNZ) and while floating on water (RMR_{water}) at varying temperatures, and percent difference in RMR_{water} relative to RMR_{air} at TNZ

Species	Mass (kg)	RMR_{air} TNZ ($W\text{ kg}^{-1}$)	T_w ($^{\circ}\text{C}$)	RMR_{water} ($W\text{ kg}^{-1}$)	Difference (%)	Reference		
Common murre	.836	7.18	20	7.30	+2	Croll and McLaren 1993		
			10	11.39	+59			
			0	17.39	+142			
Thick-billed murre	.803	8.60	20	8.84	+3	Croll and McLaren 1993		
			10	13.29	+55			
			0	20.99	+144			
Cassin's auklet	.165	10.22	20	12.47	+22	This study		
			10	16.07	+57			
			0	19.67	+92			
Common eider	1.666	3.68	20	3.83	+4	Jenssen et al. 1989		
			10	4.58	+24			
			0	5.48	+49			
Long-tailed duck	.490	5.60	20	5.59	+0	Jenssen and Ekker 1989		
			10	6.87	+23			
			0	11.97	+114			
Mallard	1.081	5.18	20	7.14	+38	Prange and Schmidt-Nielsen 1970		
			8	8.10	+56			
Great cormorant	2.56	3.10	12.6	14.10	+355	Schmid et al. 1995		
Double-crested cormorant	2.10	4.59	15	10.83	+165	Enstipp et al. 2006		
			8	14.62	+219			
European shag	1.67	4.73	5–13	19.37	+310	Enstipp et al. 2005		
Adélie penguin	4.01	3.75	4	8.36	+123	Chappel and Souza 1988 Culik et al. 1991		
Humboldt penguin	3.6	3.80	19	5.99	+58	Luna-Jorquera and Culik 2000		
Little penguin	1.157	3.12	20	6.40	+105	Baudinette et al. 1986; Baudinette and Gill 1985		
			10	8.50	+172			
			1.0	4.93	20		7.10	+44
			10	9.24	+87			
Black-legged kittiwake	.295	7.89	0	23.72	+381	Stahel and Nicol 1982		
			12.5	12.09	+53			

Note. Where possible, measures of RMR_{air} at TNZ and RMR_{water} at different temperatures were derived from the same study using linear regressions of RMR_{water} versus water temperature (T_w , $^{\circ}\text{C}$). Other values were taken from studies using similar experimental conditions. All values were measured on adult postabsorptive birds by oxygen consumption. Values presented are based on direct measurements (see Table 1 and 2) or extrapolated from linear regressions of RMR_{water} as a function of T_w . For common murre, RMR_{water} ($W\text{ kg}^{-1}$) = $17.39 - 0.60T_w$ (Croll and McLaren 1993); thick-billed murre, RMR_{water} = $20.99 - 0.77T_w$ (Croll and McLaren 1993); Cassin's auklet, RMR_{water} = $19.67 - 0.36T_w$ (this study); common eider, RMR_{water} = $5.48 - 0.09T_w$ (Jenssen et al. 1989); long-tailed duck, RMR_{water} = $11.87 - 0.50T_w$ (Jenssen and Ekker 1991); double-crested cormorant, RMR_{water} = $19.48 - 0.58T_w$ for 8° – 16°C (Enstipp et al. 2006); little penguin, RMR_{water} = $10.3 - 0.16T_w$ for $>10^{\circ}\text{C}$, or RMR_{water} = $23.72 - 1.49T_w$ for $<10^{\circ}\text{C}$ (Stahel and Nicol 1982).

gesting birds are resting on the water surface, which they can do for much of a 24-h period, thermal substitution is not an option and extra energy must be used to thermoregulate.

Diving birds often spend far more time resting on water than actively diving (Falk et al. 2000; Systad et al. 2000; Yoda et al. 2001; Tremblay et al. 2003, 2005). Thus, valid estimates of RMR on water become critical to models of energy costs, and to resulting estimates of the extent and quality of habitat needed to support the birds (Lovvorn et al. 2009). We have shown that effects on RMR of being on water cannot be estimated accurately by simple allometry over a wide range of body masses and taxa. Responses of RMR to air and water temperature, as

well as to body mass, differ substantially among major taxa of diving birds. We have further emphasized that differing experimental conditions and especially behavioral state of the birds can cause substantial variation in results among studies, and these aspects should be carefully considered when choosing values for energetics models. Far more data are needed to confirm the patterns among taxa explored here. However, our initial survey should provide a context for assessing different measurements, so that seemingly anomalous values can be recognized and their validity or relevance assessed. Above all, the consequences of values used to ecological interpretation should always be considered.

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