

Diving metabolism and thermoregulation in common and thick-billed murre

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Abstract. The diving and thermoregulatory metabolic rates of two species of diving seabird, common (*Uria aalge*) and thick-billed murre (*U. lomvia*), were studied in the laboratory. Post-absorptive resting metabolic rates were similar in both species, averaging $7.8 \text{ W} \cdot \text{kg}^{-1}$, and were not different in air or water (15–20 °C). These values were 1.5–2 times higher than values predicted from published allometric equations. Feeding led to increases of 36 and 49%, diving caused increases of 82 and 140%, and preening led to increases of 107 and 196% above measured resting metabolic rates in common and thick-billed murre, respectively. Metabolic rates of both species increased linearly with decreasing water temperature; lower critical temperature was 15 °C in common murre and 16 °C in thick-billed murre. Conductance (assuming a constant body temperature) did not change with decreasing temperature, and was calculated at $3.59 \text{ W} \cdot \text{m}^{-2} \cdot ^\circ\text{C}^{-1}$ and $4.68 \text{ W} \cdot \text{m}^{-2} \cdot ^\circ\text{C}^{-1}$ in common and thick-billed murre, respectively. Murre spend a considerable amount of time in cold water which poses a significant thermal challenge to these relatively small seabirds. If thermal conductance does not change with decreasing water temperature, murre most likely rely upon increasing metabolism to maintain body temperature. The birds probably employ activities such as preening, diving, or food-induced thermogenesis to meet this challenge.

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Abbreviations:

ADL, aerobic dive limit; BMR, basal metabolic rate; FIT, food-induced thermogenesis; MHP, metabolic heat production; MR, metabolic rate; PARR, post-absorption resting rate; RMR, resting metabolic rate; RQ, respiratory quotient; SA, surface area; STPD, standard temperature and pressure (25 °C, 1 ATM); T_a , ambient temperature; T_b , body temperature; T_{LC} , lower critical temperature; TC, thermal conductance; V_{O_2} , oxygen consumption rate; W , body mass

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Introduction

Alcids are wing-propelled diving seabirds which range from northern temperate to high arctic oceans. Although similar to penguins in being wing-propelled divers, alcids retain the ability to fly. This has probably limited morphological adaptations for aquatic life. Flightlessness has allowed penguins to: (1) reduce the size of their wings to function as effective hydrofoils (Hui 1988), and (2) increase body size which may aid in both thermoregulation in water and increasing O_2 stores for diving. In contrast, the constraints of flight in alcids have limited the reduction of wing size and increase in body size they may achieve.

Gabrielsen et al. (1988) measured the MR of one species of alcid, the thick-billed murre (*Uria lomvia*), at various air temperatures and found that murre have a RMR in air which is significantly higher than that predicted by allometric equations. They speculated that the high latitude distribution, diving foraging strategy, and overall high activity level found in murre resulted in an elevated RMR. The MR of murre may further be influenced by the fact that they spend at least half of their lives at sea, on or under the water. Water has a specific heat 4000 times greater than that of air and a thermal conductivity 25 times that of air. Thus, thermoregulation on or under the water may pose a significant metabolic challenge for murre. During the winter, common murre are found in waters with temperatures less than 5 °C (Tuck 1961) while thick-billed murre are found feeding in pack-ice waters with temperatures less than 0 °C (Bradstreet and Brown 1985). Kooyman (1976) observed that emperor penguins, roughly 30 times the size of murre, shiver in sea water at -1.85 °C. Cold adaptation in homeotherms may occur through increasing insulation

or increasing MHP (Scholander 1950). Penguins exhibit a number of adaptations to reduce heat loss to their environment: (1) a dense plumage (Kooyman et al. 1976) which prevents water from penetrating to the skin during compression, and (2) a reduced surface-to-volume ratio which serves to reduce heat loss. Bedard (1985) noted that murrelets also have a relatively dense plumage, but because of their smaller size they have a surface-to-volume ratio much higher than that found in the polar penguins. Thus, the rate of heat loss in murrelets may be greater, leading to a higher metabolic cost for thermoregulation.

Common and thick-billed murrelets are among the smallest diving homeotherms, foraging as deep as 180 m and 210 m, respectively (Piatt and Nettleship 1985; Croll et al. 1992). This remarkable diving ability raises the question of metabolism during the dive. Estimates of ADL, when used in conjunction with measurements of diving behavior in the field, serve as a framework with which to evaluate the physiological and ecological strategies employed by the free-ranging bird in exploiting prey resources. Calculation of the ADL requires estimates of the O_2 stores of the animal and the diving MR. O_2 stores have been estimated using laboratory physiological measurements in a number of diving seabirds [review: Kooyman (1989)], including thick-billed murrelets (Croll et al. 1992). The MR of voluntarily diving birds, however, has been measured only in tufted ducks, *Aythya fuligula* (Woakes and Butler 1983) and Humboldt penguins, *Spheniscus humboldti* (Butler and Woakes 1984).

The purpose of this study was: (1) to measure the diving MR of murrelets as an aid to understanding the diving behavior and physiology of free-ranging murrelets, and (2) to examine the thermal challenge imposed upon murrelets by their cold temperate to high arctic marine habitat, and examine strategies these birds may employ to cope with this challenge.

Materials and methods

Experimental birds. Eight adult common murrelets weighing 0.836 ± 0.076 kg and six 2-year-old thick-billed murrelets weighing 0.803 ± 0.050 kg were used in the study. The birds were collected as chicks from their natal site (Pribilof Islands, Bering Sea, and Coats Island, Hudson Bay; common and thick-billed murrelets, respectively), hand reared at Sea World, San Diego, Calif., USA, and maintained indoors in a 365-m² enclosure specially designed to house alcids. Within the enclosure was a pool (15 m \times 6 m \times 2 m deep) containing filtered sea water at 5 °C. Air temperature was maintained at 14 °C. The birds were fed a daily diet of smelt, herring, and krill supplemented by vitamins. While housed in this enclosure the birds spent most of their time in the water, diving frequently.

Physiological data were taken at the Physiological Research Laboratory, Scripps Institution of Oceanography, La Jolla, Calif., USA. There the birds were maintained in a pool (15 m \times 8 m \times 8 m deep) with a flow-through seawater system. Water temperature in the pool averaged 20 ± 1.2 °C. The birds dived regularly for food placed at the bottom of the tank in the corner opposite a floating 1 m \times 2 m platform. Animals were fasted at least 12 h before measurement of PARR.

Metabolic rate measurement. MR was measured with an open flow-through system using an Applied Electrochemistry S3A/l oxygen

analyzer. Air was pumped through the system with a variable-flow pump at a constant rate measured by a calibrated gas meter (American Meter) connected to the inlet port of the metabolic chamber. Air flow was adjusted to maintain O_2 levels above 19%, and averaged $12 \text{ l} \cdot \text{min}^{-1}$. An aliquot of expired gas was continuously removed from the outlet flow, CO_2 was removed (Baralyme), water vapor was removed (Drierite), and O_2 content was determined. The analyzer was calibrated every 40 min with dry ambient air (20.94% O_2 and 0.03% CO_2) and the system was checked for leaks and accuracy before each experimental period by N_2 gas dilution. Percent O_2 values were logged every 10 s using an 8-bit analog-to-digital converter connected to an Apple II personal computer. $\dot{V}O_2$ was calculated using the equation of Depocas and Hart (1957). All values were corrected to STPD. During each 40-min run, at least 10 min of steady-state $\dot{V}O_2$ ($\dot{V}O_2$ not varying by more than 15%) was used as a sample for the run.

Metabolic rates in air. RMR in air was measured in a rectangular airtight Plexiglass chamber (0.5 m \times 0.5 m \times 0.7 m) with a wire grate flooring. T_a within the chamber was maintained at 20 °C [demonstrated by Gabrielsen et al. (1988) to be within the thermoneutral zone of murrelets]. Measurements were taken in the evenings between 22:00 and 02:00 hours, the rest phase of the birds' diurnal cycle. During measurements, the chamber was covered with a cloth to prevent the bird from looking out. The activity of the bird in the chamber was monitored through a small slit in the cloth.

Metabolic rates in water. MR of birds resting on the water surface was measured in an insulated water tank (2.5 m \times 0.75 m \times 1.5 m deep). Water temperature in the tank was adjusted and maintained using an external refrigerator unit with a return pump system. The bird floated in a 0.7 m diameter Plexiglass dome set in an insulated frame. The dome was covered to prevent the bird from looking out. T_a in the dome did not differ from the water temperature by more than 2 °C. T_{LC} was determined from the intersection of the line of RMR in the thermoneutral zone with the regression line of MR at low T_a .

Diving metabolism. Diving MR was measured in a similar manner to that used by Butler and Woakes (1984). For the diving experiments, the entire surface of the pool at Scripps Institution of Oceanography was covered with netting to a depth of 3 cm, except for an area in one corner which was covered by a Plexiglass dome (1.1 m \times 0.6 m \times 0.3 m) set in a wooden frame. The chamber was large enough to allow the bird to move freely within it. Food was introduced in the diagonally opposite corner, requiring the birds to dive in order to feed. The birds would often dive consistently in search of food prior to its introduction, allowing the measurement of diving MR on post-absorptive birds. Behavior was monitored continuously throughout the experimental period. Generally, the birds dived in bouts lasting 2–10 min. Diving MR was only calculated for bouts lasting 10 min or longer. Dive/surface times were recorded as a measure of diving effort, while subsurface wing beat frequencies were recorded by visual observation from the surface as a measure of swimming effort. Wing beat frequency was calculated as the number of wing beats over the entire dive duration. The wing beat frequency for all dives was averaged as a measure of swimming effort. Absorptive RMR was measured when the birds rested for more than 10 min at least 10 min after a feeding bout. The birds were maintained in the experimental setup, without the dome in place, for at least 2 weeks prior to measurements.

Thermal conductance. TC for both species were calculated using the equation:

$$TC = \frac{MHP}{(T_b - T_a) \cdot SA}$$

where TC = thermal conductance ($W \cdot m^{-2} \cdot ^\circ C^{-1}$), MHP = metabolic heat production (W) calculated using the conversion factor of

$MHP = \frac{\dot{V}O_2(\text{ml} \cdot \text{s}^{-1})}{20.1(\text{J} \cdot \text{ml} \text{O}_2^{-1})}$, T_b = body temperature ($^{\circ}\text{C}$), T_a = ambient temperature ($^{\circ}\text{C}$), and SA = surface area (m^2). SA was estimated using the Meeh equation where $SA = 10 W^{0.67}$ (Drent and Stonehouse 1971), where W is body mass in grams and SA is in cm^2 . T_b was assumed to remain constant at 38.9°C (Johnson and West 1975).

In calculating energy expenditure from $\dot{V}O_2$, a RQ of 0.8 was assumed, and a conversion coefficient of $20.1 \text{ kJ} \cdot \text{l} \text{O}_2^{-1}$ was used (Gessaman and Nagy 1988); $1 \text{ kJ} = 0.2389 \text{ kcal}$.

Results

Metabolic rates of various activities

The results of measurements of the MRs of various activities are shown in Fig. 1. PARRs in both air and water for both common and thick-billed murres were not significantly different ($F = 0.74$, $P > 0.05$). Overall mean PARR was $7.8 \pm 0.7 \text{ W} \cdot \text{kg}^{-1}$.

Common murres

ANOVA comparisons of common murre MRs during different activities and feeding status showed that feeding, diving, and preening significantly raised MRs above resting rates in air and water ($F = 28.50$, $P < 0.01$). PARRs in air at 20°C were not different from those in water between 15 and 20°C (within the thermoneutral zone). Multiple comparisons revealed that absorptive RMR at thermoneutral water temperatures was higher than PARR in both air and water. Diving MR (including dives and pauses) was significantly higher than PARR in air and water and absorptive RMR in water. Preening MR was significantly higher than PARR in air and water and absorptive RMR in water. Common murres averaged 45% of each dive bout under water, with dive durations averaging 23 s. Absorptive diving MR was not significantly greater than post-absorptive diving MR. Feeding caused a 36% increase, diving caused an 82%

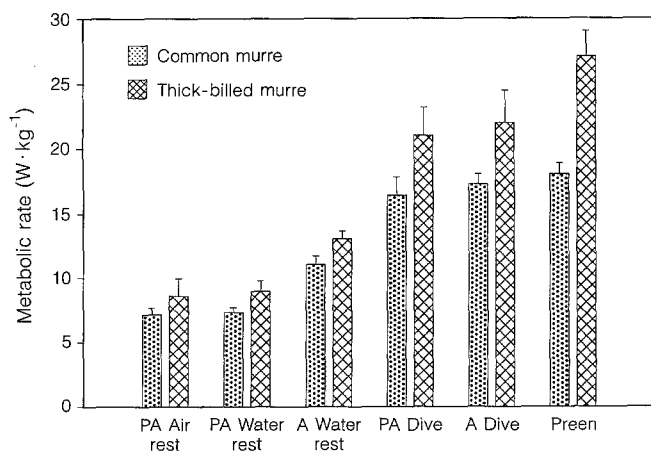


Fig. 1. Measured metabolic rates of post-absorptive (PA) and absorptive (A) common (stippled bars) and thick-billed (hatched bars) murres resting in air, resting in water, diving, and preening

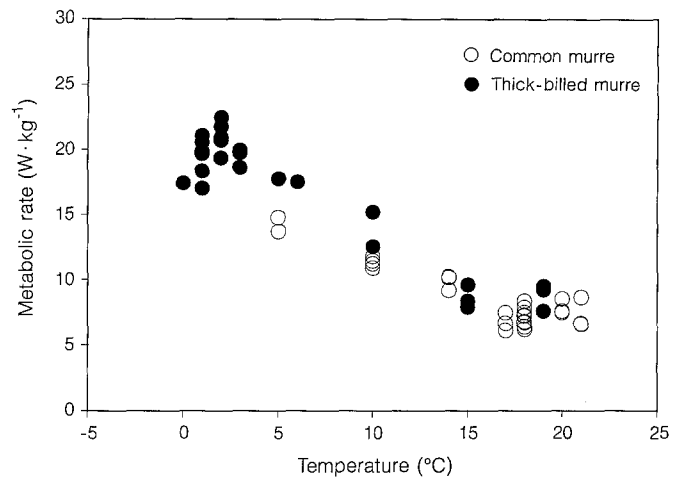


Fig. 2. Metabolic rates of post-absorptive common (open circles) and thick-billed (closed circles) murres in water at various temperatures

increase, and preening caused a 107% increase in measured RMR in air and water.

Thick-billed murres

ANOVA comparisons of thick-billed murre MRs also showed that feeding, diving, and preening significantly raised MR above PARR in air and water ($F = 88.02$, $P < 0.01$). Multiple comparisons revealed that absorptive MR was higher than PARR in air and water, while diving MR was significantly higher than PARR in air and water and absorptive RMR in water. Thick-billed murres averaged 62% of each dive bout under water, with dive durations averaging 41 s. Absorptive diving MR was not significantly different from post-absorptive diving MR. Feeding resulted in a 49% increase, diving a 140% increase, and preening a 196% increase in measured RMR in air and water.

Thermoregulation

Thermoregulatory MRs of murres floating on water are plotted in Fig. 2. Both species showed similar responses to decreasing water temperature. T_{LC} in common murres was estimated at 15°C , while thick-billed murres T_{LC} was estimated at 16°C . The equation relating MR to decreasing temperature was: $\text{MR} (\text{W} \cdot \text{kg}^{-1}) = 17.39 - 0.60 (T^{\circ}\text{C})$ ($r^2 = 0.93$) in common murres, and $\text{MR} (\text{W} \cdot \text{kg}^{-1}) = 20.99 - 0.77 (T^{\circ}\text{C})$ ($r^2 = 0.82$) in thick-billed murres. The slopes of these regressions were significantly different ($t = 10.43$, $P < 0.01$).

Thermal conductance

TC (assuming constant body temperature) for both species did not change with decreasing temperature (Fig. 3). Mean (\pm SD) TC for common murres was calculated at

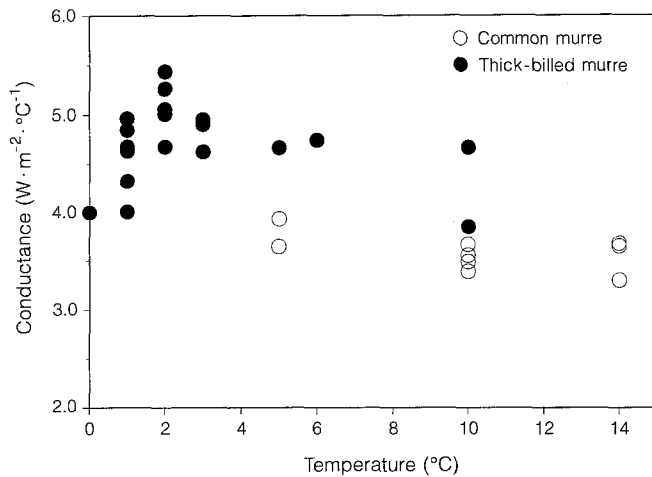


Fig. 3. Conductance of common (open circles) and thick-billed (closed circles) murre in water at various temperatures

$3.59 \pm 0.18 \text{ W} \cdot \text{m}^{-2} \cdot \text{°C}^{-1}$, while TC for thick-billed murre averaged $4.68 \pm 0.42 \text{ W} \cdot \text{m}^{-2} \cdot \text{°C}^{-1}$; these means were significantly different ($t=9.73$, $P<0.01$).

Discussion

Energy costs of different activities have been used to elucidate the foraging strategies, behavior, and ecological requirements of a wide range of bird species [reviews by King (1974) and Kendeigh et al. (1977)]. Allometric estimates of the energetic cost of various activities have been used to examine the importance of seabirds as predators in marine ecosystems (Wiens and Scott 1975; Furness 1978), estimating that seabirds may consume 22–29% of the local production of prey species each year. A weakness of these models has been that the activity costs of seabirds, except penguins, are not well known. As a result, seabird energetic models have relied almost entirely on metabolic estimates developed for terrestrial birds (Kendeigh et al. 1977). Laboratory measurement of specific activities of seabirds allows more valid estimates of individual and population energetic requirements through time-budget models.

The mean, post-absorptive RMR of common murre in air obtained in this study (6.0 W per bird; Fig. 1) was 11% lower than the value obtained by Johnson and West (1975) for post-absorptive common murre in air (6.8 W

per bird). The mean, post-absorptive RMR of thick-billed murre in air obtained in this study (6.9 W per bird; Fig. 1) was 3% higher than the 6.8 W per bird measured by Johnson and West (1975) and 26% higher than the value obtained by Gabrielsen (1988) for post-absorptive thick-billed murre resting in air (5.1 W per bird). Although there are differences in the RMR values for murre measured by these studies, the measured MRs in all cases were 1.3–2.2 times the values predicted for murre by allometric models (Table 1). This differs from penguins where measured and predicted MRs are generally in agreement (Stahel and Nicol 1982). Two possible explanations may account for the observed rates: (1) the standard requirements for resting MRs were not achieved in the three murre studies, or (2) elevated RMRs are real and adaptive for birds living in high-latitude, thermally rigorous habitats. This would support the hypothesis of Weathers (1979) that the standard MR of high-latitude, cold climate birds tends to be higher than that of low latitude species.

True BMR measurements require that: (1) the animal is post absorptive and resting, (2) measurements are made within the animals' thermoneutral zone, and (3) measurements are made during the inactive phase of the animals' light cycle. All three conditions were satisfied by our study and that of Johnson and West (1975). Gabrielsen et al. (1980) satisfied the first two conditions and found that their high latitude study site led to no diurnal differences in MR. All three murre studies employed methods similar to those used to derive the allometric equations and to measure penguin RMR. These results suggest that the high RMR we measured is real.

Kooyman et al. (1976) suggested that the elevated MR they observed in Adelie penguins may be due to their need to thermoregulate in water. However, when compared to the alpha equation of Aschoff and Pohl (1970) for birds during the active phase of their diurnal cycle, the RMR of Adelie penguins is not different from that predicted. Recently, Lavigne et al. (1986) argued against the hypothesis that the higher MRs of marine mammals were adaptive for life in water, proposing that the observed elevated resting MRs were an artifact of studying non-resting or excited animals. Although apparently resting, the murre in the present study may have been excited. Gabrielsen et al. (1988) reported that the birds in his study were most likely excited, precluding the measurement of true BMR. Thus, speculation on the adaptive significance of elevated RMRs in murre must be made with caution.

Table 1. Predicted and measured metabolic rates (watts per bird) for common and thick-billed murre

Species	Weight (kg)	This study Air	Water	Gabrielsen et al. (1988)	J&W (1975)	L&D (1967)	A&P (1970)	Ellis (1984)
Common murre	0.836	6.0	6.1	—	6.8	3.3 (208)	3.9 (154)	3.9 (154)
Thick-billed murre	0.803	6.9	7.1	5.1	6.8	3.2 (216)	3.8 (182)	3.8 (182)

Values in parenthesis represent percentage difference of values measured in this study from predicted values calculated from the equations of Lasiewski and Dawson (1967): $H_{sm} = 3.78 M_b^{0.723}$; Aschoff and Pohl (1970) (active): $H_{sm} = 4.41 M_b^{0.729}$; Ellis (1984): $H_{sm} = 4.41 M_b^{0.721}$

We found no difference between RMR in air and water within the thermoneutral zone in both species. This differs from the findings of Stahel and Nichol (1982) who found no thermoneutral zone in water for little penguins (*Eudyptula minor*). They observed that MR increased gradually with decreasing water temperature until a critical temperature of 10 °C, below which MR increased rapidly. In the present study murre MR was constant above 15 °C; below that point, MR increased linearly in both species (Fig. 2). The slope of this rise (0.60 and 0.77) in common and thick-billed murres floating on water was considerably steeper than the 0.17 slope of the MR of murres in air at $T_{a,s}$ below T_{LC} measured by Gabrielsen et al. (1988). This is most likely due to the higher TC of water.

It is reasonable to expect an abrupt increase in MR below T_{LC} in water, assuming TC does not change. To maintain waterproofing, murres are probably not able to increase the thickness of their insulative feather layer and thereby reduce the TC of their plumage in colder water. We observed no change in TC in the murres with decreasing temperature (assuming that T_b remained constant). Stahel and Nichol (1982) found that TC in little penguins decreases with decreasing temperature, and speculated that TC is reduced in little penguins in water through peripheral vasoconstriction which reduces the size of the peripheral shell. Whether a similar mechanism occurs in murres awaits measurements of body core and surface temperatures with decreasing T_a .

The calculated TC of murres in water was 2.69 and 3.51 $W \cdot m^{-2} \cdot ^\circ C^{-1}$ in common and thick-billed murres, respectively. These values are considerably lower than those measured for penguin species immersed in water [which range from 4.00 to 14.43 $W \cdot m^{-2} \cdot ^\circ C^{-1}$; Barre and Roussel (1986)]. Murres may minimize TC in water by: (1) being relatively buoyant, minimizing the SA in contact with water, (2) withdrawing the legs and feet into the feathered area to avoid contact with the water, (personal observations) (3) having contour feathers which are relatively long and dense, able to trap a thicker layer of air, and (4) keeping the wings, which have a large SA, out of the water while at rest.

Stahel and Nichol (1982) found the TC of little penguins in air was 1.93 $W \cdot m^{-2} \cdot ^\circ C^{-1}$, while Kooyman et al. (1976) found the TC of Adelie and gentoo penguin pelts in air to be 1.75 and 1.93 $W \cdot m^{-2} \cdot ^\circ C^{-1}$, respectively. Gabrielsen et al. (1988) found the TC of thick-billed murres was 1.44 $W \cdot m^{-2} \cdot ^\circ C^{-1}$ in air. Using this value as a comparison, immersion in water causes a 186–243% increase in TC in murres. During diving, murres may experience an even greater increase in TC due to compression of the insulative layer with depth (Kooyman et al. 1976).

The observation that murres are not thermally neutral in water temperatures less than 15 °C is ecologically important. The water temperatures throughout the home range of murres are never greater than 15 °C. Thus, murres must maintain an elevated MR in order to maintain T_b when resting on the water surface. Compared to penguin species living at similar latitudes, murres are

considerably smaller and thus have a higher surface-to-volume ratio. Stahel and Nichol (1982) hypothesized that the small size of little penguins may limit their southerly distribution. Since TC does not appear to change with decreasing temperature in murres, strategies to increase MHP in order to maintain their T_b in cold arctic waters must be employed.

Absorptive MRs were 51% and 45% higher than those of post-absorptive common and thick-billed murres, respectively. Baudinette et al. (1986) studied the effects of food-induced thermogenesis (FIT), or specific dynamic action, on the MR of little penguins. They found that feeding increased RMR by 87%. This led them to speculate that FIT may be important in thermoregulation in small aquatic species. Costa and Kooyman (1984) studied the metabolism of California sea otters (*Enhydra lutris*) and found that a post-absorptive sea otter is not thermally neutral at water temperatures below 20 °C. Their measurement showing that FIT increased MR by 54% led them to the conclusion that FIT may allow longer periods of rest between feeding bouts while it replaced heat otherwise required through activity or shivering. By raising the MR of common and thick-billed murres to 11.0 $W \cdot kg^{-1}$ and 11.72 $W \cdot kg^{-1}$, respectively, FIT would allow the birds to remain thermally neutral in water temperatures of about 10 °C. Although insufficient for wild birds to maintain T_b in water at 0–5 °C in which they are found, this supplemental heat may decrease shivering or increase the time between activity bouts. Wilson and Culik (1991), in contrast, have suggested that the post-feeding increase in MR observed in Adelie penguins (*Pygoscelis adeliae*) is due to heating of the ingesta rather than specific dynamic action. The same mechanism may explain the increase in MR in murres. The reason for the increase in MR due to feeding is important: an increase due to heating of food would represent an additional thermoregulatory burden, whereas an increase due to specific dynamic action would aid in thermoregulation.

Preening was the most costly activity measured in murres, leading to an average increase of 145 and 196% of RMR in common and thick-billed murres, respectively. The intensity of preening is highly variable, and this may explain the large differences observed in the mean cost of preening in the two species. This increase in MR due to preening may aid murres in maintaining T_b in cold water. In addition, preening helps in maintaining the integrity of the plumage and increases the thickness of the insulative layer. Thus, it is likely an important thermoregulatory behavior in murres.

The MR of voluntarily diving birds been measured only in Humboldt penguins (Butler and Woakes 1984) and tufted ducks (Woakes and Butler 1983). Whereas diving in tufted ducks increased MR to 3.47 times that of rest, diving in Humboldt penguins only raised MR to 1.26 times resting levels and this increase was not significant. Diving in common and thick-billed murres led to an increase of 1.8 and 2.4 times RMR, respectively. Common murres spent 45% of dive bouts under water making dives averaging 23 s. This is less than that ob-

served by Wanless et al. (1988) in freely diving wild common murrelets where 63% of dive bout time was below the surface with dives averaging 67 s. Thick-billed murrelets spent 62% of laboratory dive bouts below the water surface making dives which averaged 41 s. This is similar to values measured in thick-billed murrelets diving freely in the wild where 65% of each dive bout is spent below the surface, and dive durations average 54.2 s (Croll et al. 1992). The differences in time spent submerged between the two species may explain the observed differences in increased MR. The subsurface wing beat frequencies of thick-billed murrelets diving in the laboratory ($1.9 \text{ strokes} \cdot \text{s}^{-1}$) were not different from those observed in wild thick-billed murrelets diving near a coastal cliff in shallow water ($1.8 \text{ strokes} \cdot \text{s}^{-1}$; D.A. Croll, personal observation). In both species, laboratory diving resulted in a higher increase (as a multiple of RMR) than that observed in penguins. Due to differences in wing morphology between penguins and murrelets, the latter may have a less efficient means of underwater propulsion. In addition, several authors have recently pointed out the cost of overcoming buoyancy in diving birds (e.g. Woakes and Butler 1983; Wilson et al. 1992). Wilson et al. (1992) found that diving birds generally have a lower volume of trapped air in their plumage. Overcoming buoyancy may be a significant cost in shallow-diving murrelets (as measured in the present study). However, murrelets diving to depth in the wild may have lower diving energetic costs since buoyancy is reduced as the layer of trapped air in the feathers is reduced by hydrostatic pressure at depth.

The cold, aquatic habitat of murrelets poses a challenge to the birds' ability to maintain T_b . Below the thermoneutral zone a bird can increase insulation or increase MR. It is difficult for an aquatic bird to increase its insulative layer when immersed in water. Moreover, increasing the insulative capabilities of the feather layer may create problems in heat dissipation as MR increases in flight. Thus, murrelets must increase MR when thermally challenged in water. Murrelets may use shivering to increase heat production, but it is likely that other methods are also used. Preening directly raises MR and may increase the insulative capabilities of the feather layer. Diving not only increases heat production, but, through prey capture, may result in FIT which would further serve to increase heat production in a bird resting at the surface.

In conclusion, both species of murrelet had similar resting, diving, and FIT MRs. RMRs were higher than those observed and predicted in other non-passerine birds. This may be an adaptation for the high-latitude, cold aquatic environment where murrelets are generally found. Murrelets must expend energy for thermogenesis in order to maintain T_b in the waters in which they are normally found. In addition to shivering preening, FIT and diving may all be mechanisms that are employed to raise MR to achieve thermal balance. The metabolic cost of diving in murrelets (as a multiple of RMR) was higher than values previously reported for penguins. The reasons for the higher diving MR observed in murrelets may be due to: (1)

higher costs to overcome buoyancy, and/or (2) a less efficient method of wing-propelled underwater locomotion due to differences in the wing morphology of murrelets and penguins.

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