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Published in:
Physiological Zoology

DOI:
[10.1086/physzool.68.6.30163797](https://doi.org/10.1086/physzool.68.6.30163797)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1995

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

de Vries, J., & van Eerden, M. R. (1995). Thermal conductance in aquatic birds in relation to the degree of water contact, body mass, and body fat: Energetic implications of living in a strong cooling environment. *Physiological Zoology*, 68(6), 1143-1163. <https://doi.org/10.1086/physzool.68.6.30163797>

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Thermal Conductance in Aquatic Birds in Relation to the Degree of Water Contact, Body Mass, and Body Fat: Energetic Implications of Living in a Strong Cooling Environment

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Source: *Physiological Zoology*, Vol. 68, No. 6 (Nov. - Dec., 1995), pp. 1143-1163

Published by: The University of Chicago Press. Sponsored by the Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology

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Thermal Conductance in Aquatic Birds in Relation to the Degree of Water Contact, Body Mass, and Body Fat: Energetic Implications of Living in a Strong Cooling Environment

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Accepted 2/21/95

Abstract

Thermal conductance of carcasses of 14 aquatic bird species was determined by the warming constant technique. The effect on thermal conductance of body mass, age, sex, fat deposits, and the degree of contact with water were studied. Only body mass and the degree of submergence in water had an effect. A negative exponential relationship between body mass and thermal conductance was found. Water contact increased the thermal conductance by a factor of 2.2 during swimming and a factor of 4.8 during diving. Leaving the water in order to reduce thermoregulatory costs is put forward as a behavioral option that might make several aquatic birds more flexible in adjusting their feeding time to meet increasing energetic requirements. Not being able to leave the water has obvious implications for both breeding and winter distributions for different-sized aquatic birds.

Introduction

Endothermic aquatic animals might be seriously affected by the thermal properties of water, because the heat capacity of water is 25 times greater than that of air. Heat loss of animals is dependent on their exposed surface area, thermal conductivity (C), and the difference between ambient temperature (T_a) and body temperature (T_b). One may wonder how birds cope with the problem of thermoregulation in their aquatic environment, because adaptation to a greater heat loss in water is not achieved by a beneficial

surface-to-volume ratio such as large sea mammals have. Many bird species (e.g., *Gaviidae*, *Podicipedidae*, *Anatidae*, *Alcidae*, and *Spheniscidae*) tolerate near-freezing water temperatures despite their small body size (Atkinson-Willes 1976; Cramp et al. 1977; Owen 1980). If thermal adaptation to the great cooling power of water exists, one might expect a lower C in air for aquatic bird species compared with terrestrial species. However, some studies indicate higher C in air for aquatic bird species (Bech 1980). Very little is known about actual C of birds while floating or diving. A few studies report increased C in birds while floating or diving that is two or five times their air C , respectively (Kooyman et al. 1976; Stahel and Nicol 1982; Jenssen, Ekker, and Bech 1989). The lack of data about heat loss of birds in air and water inspired us to measure C over a wide range of species. Experiments were conducted comparing the C of birds in a standing posture in air, a partially submerged swimming posture, and a wholly submerged diving posture. In addition to the effect of body mass (m), effects of sex and age on C were also studied.

Material and Methods

In this study we used 113 carcasses of 14 aquatic bird species that were collected from the freshwater lakes IJsselmeer and Markermeer and the adjacent reed marsh, Oostvaardersplassen, in The Netherlands (for detailed information, see appendix). The carcasses were obtained from local fishermen from August to March. The diving ducks (*Aythya*), grebes (*Podiceps*), mergansers (*Mergus*), and cormorants (*Phalacrocorax*) had been drowned accidentally in fishing gear. Only freshly caught birds with intact and entirely down-dry plumage were used. Dabbling ducks and geese (*Anas*) were collected during a *Clostridium botulinum* epidemic in the reed marsh, where the birds had died a few hours after drinking the contaminated water.

After collection, the birds were cleaned if necessary. Their plumage was dried for 2 h in a forced ventilated oven at 30°C. After plumage drying the birds were used for experiments or were individually stored in tied plastic bags in a freezer at -20°C until measurements began. The carcasses were stored at -20°C, because in tufted ducks (*Aythya fuligula*) and great crested grebes (*Podiceps cristatus*) no effect of storage for 2 mo was found on C compared with direct measurement (T -test; tufted duck, *A. fuligula*, $df = 16$, $P = 0.39$, not significant [n.s.]; great crested grebe, *P. cristatus*, $df = 10$, $P = 0.22$, n.s.).

Carcass masses ranged from 0.25 to 3.5 kg. Birds were aged and sexed by gonadal and plumage inspection distinguishing between juvenile (first winter) and adult (after first winter).

Whole-body C 's were obtained by a warming curve analysis of the carcasses (Morrison and Tietz 1957; Herreid and Kessel 1967). Thermal conductance was expressed relative to m and not surface area, because surface area is difficult to obtain in the swimming and diving postures. Thermal conductance ($\text{kJ} \cdot ^\circ\text{C}^{-1} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$) was estimated by multiplying the warming constant with the specific heat of mammalian tissue ($3.47 \text{ J} \cdot \text{g}^{-1}$; Morrison and Tietz [1957]). Warming constants were obtained from the slope of the natural logarithm of the difference between T_b and T_a ($\ln (T_b - T_a)$) versus time. The difference between T_b and T_a was read every 30 min in the standing and swimming experiments but was read every 15 min in the diving experiment. The time interval over which C 's were computed was 7, 5, and 3.5 h in the standing, swimming, and diving postures, respectively. The difference between T_b and T_a was continuously recorded with calibrated thermocouples. The thermopotential of the thermocouple was amplified by a micrograph recorder (BD7, Kipp and Sons), giving a scale deflection of 0.5 mV/100 scale divisions resulting in an accuracy of the readings of 0.08°C .

The measuring point of the thermocouple was inserted into the intestinal tract and placed anteriorly as far as the liver lobes. With the aid of a small glass rod, the intestinal tract was widened to improve the insertion of the thermocouple.

The C 's were measured in an unventilated, isolated room in the central part of the laboratory that had a constant air temperature of 20°C . In this room the maximal temperature change of the air that could occur during the experiments was $0.2^\circ\text{C}/12 \text{ h}$. Change in air temperature was checked every hour from the start to the end of an experiment. The air and water temperatures were read to the nearest 0.05°C with a mercury precision thermometer (Landsberger; $18^\circ\text{--}35^\circ\text{C}$).

Thermal conductance of the carcasses was measured in air and then in water while swimming and diving. For 112 birds C was measured in air. For 106 birds C was measured only when standing and swimming, and for 50 birds C was measured for all three postures (see appendix). A day prior to the experiment, the carcasses were thawed for approximately 10 h. After thawing the carcasses were cooled for 15 h in a refrigerator. Only carcasses of species weighing more than 1.5 kg were cooled longer (i.e., 24 h).

According to the law of Newtonian cooling and warming, the cooling or warming constant (derived as described above) is not affected by the initial temperature of the carcass but is affected by the thermal homogeneity of the carcass (Morrison and Tietz 1957). Therefore, prior to measurement

carcasses were checked for their temperature homogeneity in the refrigerator by measuring the temperature in the intestinal tract from deep inside (between the liver lobes) to the anus with a precision mercury thermometer (Landsberger; -1° to 18°C). Only carcasses that were thermally homogeneous (i.e., without a temperature gradient between core and skin) with T_b 's between 1° and 4°C were used for measurements; otherwise, they were cooled longer. The same procedure was followed prior to taking the swimming and diving measurements.

During measurements in air at 20°C , the carcasses were laid on their backs on a wire mesh ($3\text{ cm} \times 3\text{ cm}$) 50 cm above a table. Tanks filled with 70 and 100 L of water were used in the swimming and diving experiments, respectively. By using large volumes of 20°C water (in an infinite heat sink) in thermal equilibrium with the surrounding air (air temperature = water temperature) during the experiments, changes in water temperature due to the cooling effect of the cold carcasses are then insignificant (0.01°C or less). The carcasses were fixed in the swimming posture by clamping their heads above the water when they were floating on the surface. The heads and legs of the carcasses were tied to rods attached to a table standard to keep them in the diving posture (head downward, body vertical, tail 15 cm below the water surface). Carcass and standard were placed under water in the 100-L tank. Water was prevented from leaking into the body cavities by sealing the throats and cloacae with 5 cm^3 glycerine and by taping the bills.

The fat content of the carcasses was gravimetrically determined by either the Soxhlet or the diffusion method. To improve the fat mass analyses, the thorax and abdomen were opened and the glycerine was removed from the throat and cloaca. The diffusion method gave reliable results in birds with m 's up to 1.5 kg. Therefore, the diffusion method was only used in these birds. The Soxhlet method was used in birds with m 's greater than 1.5 kg. Oven-dried carcasses (2 d at 100°C and 5 d at 80°C) were weighed before and after fat extraction to obtain the fat and fat-free masses. We dried at these temperatures because drying at 100°C in chickens (Kirkwood 1981) and 95°C in rats (Leppington, Djolteto-Nathey, and Wheeler 1978) did not reduce the fat content by causing loss of volatile components soluble in petroleum ether. In addition, Kirkwood (1981) found that in samples dried for 8 d at 60°C to constant weight, dry matter content was overestimated by residual water. In the diffusion method the carcasses were soaked in petroleum ether, and the fat masses of 30 carcasses were determined per session. Therefore, the carcasses were individually placed in loosely woven nylon bags to keep them separate during the fat extractions. The diffusion method was carried out in five extraction steps. In each step 20 L of petroleum ether was used per 30 carcasses. The first fat extraction step was performed in

petroleum ether that had been previously used four times. The second extraction step was performed in petroleum ether previously used three times, and so on. The fifth and final fat extraction step was performed in clean petroleum ether. The total time of the five diffusion steps was 7 d. The first four extraction steps took 1 d per step, and the fifth and final step took 3 d. After fat extraction the carcasses were dried in a vacuum oven at 60°C at a pressure of 3–5 cmHg for 24 h and weighed to the nearest 0.1 g. Fat masses (g) obtained by the diffusion method were corrected with the following regression: $\text{fat mass}_{\text{soxhlet}} = \text{fat mass}_{\text{diffusion}} \cdot 1.0344 + 2.2790$ ($n = 61$, $\text{SE}_{\text{slope}} = 0.01261$, $r^2 = 0.991$). This regression was obtained from 61 carcasses (0.2–1.5 kg) for which the fat mass was first determined by the diffusion method followed by the Soxhlet method.

Descriptive statistics, regressions, and F -tests were determined according to Sokal and Rohlf (1981).

Results

Thermal conductance was positively correlated with the degree of contact with water. In table 1 the average C 's of the various species, age, and sex classes found for the standing posture in air and the swimming and diving postures in water are sorted according to increasing m . The respective C 's of the swimming and diving postures were 2.0–2.5 and 4.8–5.0 times the value of the standing posture in air.

For each posture allometric relationships between m and C were calculated to obtain the interspecies lines (fig. 1). A strong negative exponential relationship between m and C was found for all three conditions (fig. 1). The allometric functions of the swimming and diving postures showed the same magnitude of elevation relative to the standing posture in air, as mentioned previously (table 1). The slopes of the three lines are not significantly different from each other (F -test), but the y -intercepts are statistically different (ANCOVA, $P < 0.00001$).

The allometric relationships between m and C did not differ significantly between the age and sex classes in each posture (F -test; table 2).

A within-species analysis was carried out for *Podiceps cristatus*, *Aythya fuligula*, and *Aythya marila*. Also within species, C decreased significantly with increasing body weight, but regressions were not significant for *Podiceps* and *A. marila* in air (fig. 2).

The fat fraction of fresh m varied between 5% and 25% for more than 95% of the birds measured. This range was typical for the annual variation for the species occurring in the study area. Regressions of the residuals for fat

TABLE 1
Thermal conductance for different species, age, and sex groups measured in three different postures

Species	Age, Sex ^a	n	m ^b (kg)	C ^c (kJ · °C ⁻¹ · h ⁻¹ · kg ⁻¹)			Ratio to Standing		
				Standing	Swimming	Diving	Standing	Swimming	Diving
<i>Anas crecca</i>	A, F	4	.279 ± .015	1.46 ± .07	3.66 ± .27	7.27 ± .45	1	2.5	5.0
<i>Bucephala clangula</i>	A, F	4	.758 ± .029	.68 ± .04	1.48 ± .08	...	1	2.2	...
<i>Aythya fuligula</i>	J, F	5	.834 ± .039	.83 ± .08	1.92 ± .26	...	1	2.3	...
<i>A. fuligula</i>	A, F	5	.922 ± .061	.85 ± .04	1.67 ± .14	...	1	2.0	...
<i>Podiceps cristatus</i>	J, M	4	.939 ± .037	.70 ± .02	1.65 ± .16	...	1	2.3	...
<i>A. fuligula</i>	A, M	10	.946 ± .035	.77 ± .03	1.68 ± .06	3.71 ± .24	1	2.2	4.9
<i>P. cristatus</i>	J, F	4	.994 ± .067	.70 ± .06	1.48 ± .06	3.37 ± .10	1	2.1	4.8
<i>P. cristatus</i>	A, M	6	1.115 ± .098	.68 ± .04	1.38 ± .08	3.40 ± .20	1	2.0	5.0
<i>Aythya marila</i>	A, F	4	1.198 ± .047	.61 ± .09	1.33 ± .06	2.94 ± .16	1	2.3	4.8
<i>Mergus serrator</i>	A, M	4	1.314 ± .031	.63 ± .03	1.31 ± .10	...	1	2.1	...
<i>A. marila</i>	A, M	5	1.431 ± .022	.50 ± .05	1.28 ± .06	2.41 ± .07	1	2.5	4.8

Note. Ellipses indicate $n < 4$ for the posture.
^a A = adult, J = juvenile, M = male, and F = female.
^b Values shown are means ± 1 SEM.
^c Values shown are means ± 1 SEM if $N \geq 4$.

Fig. 1. Relationship between m (kg) and C ($\text{kJ} \cdot ^\circ\text{C}^{-1} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$) in various aquatic birds. Thermal conductance was measured for the standing posture in air (filled circles), for the swimming posture (open triangles), and for the diving posture in water (filled squares). The lines represent $C = am^b$ obtained from regression of $\log(C)$ on $\log(m)$ for the standing posture in air ($C = 0.705m^{-0.461}$, $r^2 = 0.577$, $SE_{\text{slope}} \pm 0.038$, $P < 0.00001$, $n = 112$), swimming posture in water ($C = 1.532m^{-0.546}$, $r^2 = 0.656$, $SE_{\text{slope}} \pm 0.039$, $P < 0.00001$, $n = 106$), and diving posture in water ($C = 3.47m^{-0.573}$, $r^2 = 0.828$, $SE_{\text{slope}} \pm 0.038$, $P < 0.00001$, $n = 50$). Species values (mean of C) are presented in the inset figure; a, *Anas crecca*; b, *Mergus albellus*; c, *Fulica atra*; d, *Bucephala clangula*; e, *Aythya fuligula*; f, *Anas platyrhynchos*; g, *Podiceps cristatus*; h, *Aythya marila*; i, *Mergus serrator*; j, *Gavia stellata*; k, *Mergus merganser*; l, *Somateria mollissima*; m, *Anser anser*; n, *Phalacrocorax carbo*.

against residuals of C were far from significant for the three postures (table 3). In addition, we looked for a more general effect by placing the residuals in a contingency table. The analyses of cell frequencies by chi-square tests were not significant for all three postures (standing, $P < 0.8$; swimming, P

TABLE 2
Effect of sex and age on parameters of allometric function ($C = am^b$) relating fresh m (g) to C ($\text{kJ} \cdot ^\circ\text{C}^{-1} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$) in aquatic bird species

Posture	Age, Sex ^a	<i>n</i>	Constant	Power	<i>P</i> Value
Standing	J, M	10	.689	$-.472 \pm .125$	<.0054
	J, F	15	.748	$-.213 \pm .094$	<.0412
	A, M	56	.709	$-.522 \pm .065$	<.0001
	A, F	31	.698	$-.409 \pm .068$	<.0001
Swimming . . .	J, M	9	.574	$-.603 \pm .143$	<.0031
	J, F	14	1.566	$-.511 \pm .115$	<.0009
	A, M	55	1.560	$-.572 \pm .063$	<.0001
	A, F	28	1.445	$-.557 \pm .071$	<.0001
Diving	J, M	3	3.519	$-.510 \pm .051$	<.0630
	J, F	8	3.564	$-.563 \pm .058$	<.0001
	A, M	26	3.464	$-.716 \pm .074$	<.0001
	A, F	13	3.527	$-.572 \pm .086$	<.0001

Note. Constant and power of the allometric function (am^b) relating C to m were obtained from regression of $\log(C)$ on $\log(m)$. Values shown are power $\pm$ SE. *P* value indicates significance of the slope (*b*) of the log-log regression (*F*-test).
^a A = adult, J = juvenile, M = male, and F = female.

< 0.2; diving, $P < 0.15$). This indicated that no relationship existed between fat content and C . Obviously, fat deposits had no effect on C in the species studied.

Discussion

Measurements of intact carcasses of aquatic birds with the warming constant technique indicated that m was an important factor influencing the level of the dry C in air and water. For practical reasons we used the warming instead of the cooling technique. The direction of heat transfer is unlikely to influence its speed, which has been demonstrated by Morrison and Tietz (1957) in a heat transfer study on three vole species. Warming or cooling of carcasses revealed the same heat transfer coefficient in these voles. Therefore, our data are completely comparable with the heat transfer data obtained with

Fig. 2. Relationship between m (kg) and C ($\text{kJ} \cdot ^\circ\text{C}^{-1} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$) in three species. The upper panel shows the diving posture in water, the middle panel shows the swimming posture, and the lower panel shows the standing posture in air. The left panel represents *Podiceps cristatus* (filled circles). The right panel represents *Aythya fuligula* (filled circles) and *Aythya marila* (filled triangles). Regressions of $\log(C)$ on $\log(m)$ for the standing posture in air: *P. cristatus*, $C = 0.672m^{-0.244}$ ($r^2 = 0.080$, $SE_{\text{slope}} \pm 0.195$, $P = 0.227$, $n = 20$); *A. fuligula*, $C = 0.740m^{-0.815}$ ($r^2 = 0.322$, $SE_{\text{slope}} \pm 0.199$, $P < 0.005$, $n = 37$); *A. marila*, $C = 0.649m^{-0.639}$ ($r^2 = 0.279$, $SE_{\text{slope}} \pm 0.296$, $P = 0.0522$, $n = 14$). Regressions of $\log(C)$ on $\log(m)$ for the swimming posture: *P. cristatus*, $C = 1.464m^{-0.573}$ ($r^2 = 0.372$, $SE_{\text{slope}} \pm 0.181$, $P < 0.01$, $n = 19$); *A. fuligula*, $C = 1.564m^{-1.009}$ ($r^2 = 0.307$, $SE_{\text{slope}} \pm 0.260$, $P < 0.001$, $n = 36$); *A. marila*, $C = 1.463m^{-0.514}$ ($r^2 = 0.513$, $SE_{\text{slope}} \pm 0.144$, $P < 0.005$, $n = 14$). Regressions of $\log(C)$ on $\log(m)$ for the diving posture in water: *P. cristatus*, $C = 3.592m^{-0.730}$ ($r^2 = 0.966$, $SE_{\text{slope}} \pm 0.041$, $P < 0.0001$, $n = 13$); *A. fuligula*, $C = 3.398m^{-1.114}$ ($r^2 = 0.538$, $SE_{\text{slope}} \pm 0.297$, $P < 0.005$, $n = 14$); *A. marila*, $C = 3.442m^{-1.067}$ ($r^2 = 0.796$, $SE_{\text{slope}} \pm 0.106$, $P < 0.0001$, $n = 9$).

TABLE 3
Least-square regression of C residuals in the standing, swimming, and diving postures on fat mass residuals

Equation	r^2	SE	P	n
$C_{\text{air-res}} = 0.002 - m_{\text{fat-res}} \cdot .129$	.0041	.199	.520	104
$C_{\text{swim-res}} = 0.028 - m_{\text{fat-res}} \cdot .469$	.0132	.412	.260	98
$C_{\text{dive-res}} = 0.100 - m_{\text{fat-res}} \cdot 2.145$	.0436	1.480	.154	48

the cooling constant technique of Herreid and Kessel (1967) on Alaskan terrestrial birds.

The present study is in agreement with the results of others that C decreases with increasing m (Herreid and Kessel 1967; Drent and Stonehouse 1971; Kendeigh, Dolnik, and Gavrilov 1977; Aschoff 1981). These studies present C as an allometric function of m such that $C = am^b$, where b is -0.536 , -0.479 , -0.484 , and -0.411 , respectively. The value of $b = -0.461$ for the aquatic birds in our study is in good accordance with b 's from the former studies. However, their corresponding values of a (in $C = am^b$; -0.474 , -0.430 , -0.332 , and -0.462 , respectively) are 1.5–2.0 times lower than the value of a (i.e., -0.705 for standing birds) of the present study. The comparison between the present data and a similar study on terrestrial birds using the same technique (Herreid and Kessel 1967) indicates that aquatic birds have higher C 's. Several metabolic studies on aquatic bird species are consistent with this (table 4). The C 's of these aquatic birds are between the predictions of the allometric lines of Herreid and Kessel (1967) and the present study. In addition, the C 's obtained by cooling curve analysis of Herreid and Kessel (1967) compare reasonably well over a large range of m 's in the compilation of C data by Drent and Stonehouse (1971; fig. 3). These data are mainly obtained by gas exchange experiments, which indicates that comparisons between various data sets of C are not hampered per se by methodological differences. The conclusion is that, contrary to what might be expected, aquatic birds do not show any adaptation in C to their cold aquatic environment.

The higher C 's in air of aquatic birds raises the question of what might be the cause of this higher level. By living in the water, birds have to prevent the plumage from losing its waterproofing capacity. Deterioration of the waterproofing capacity of the plumage severely increases C in water. We have to rely on data on mammals to get an idea of this effect. During diving

the C 's of the fresh carcasses of two vole species, *Sorex palustris* and *Sorex cinereus*, and two small mammals, *Zapus princeps* and *Peromyscus maniculatus*, with artificially water-soaked fur was 9.1 times their C in air instead of 4.6 times C with intact, dry furs (Calder 1969). It is obvious that a twofold increase of the C due to losses of waterproofing capacities must have a great impact on thermoregulatory costs. The waterproofing capacity of the plumage of birds is mainly attributable to the structure of the feather plumage and is optimal when the plumage structure remains intact (Rijke 1969). We suggest that the greater destructive forces of water movements have led in aquatic birds to structural adaptations of the plumage such as thicker shafts, barbs, and barbules of feather, causing a stiffer plumage. These adaptations might explain the higher C 's of aquatic birds in air compared with those of terrestrial ones, but it is probably the best solution for their aquatic way of life.

In animals contact with water elevates their C . An approximately twofold increase of the C during swimming compared with the C in air of the present study (table 2) is also found in metabolic studies of *Somateria mollissima* (Jenssen et al. 1989, 1990), *Clangula hyemalis* (Jenssen and Ekker 1989), and *Eudiptula minor* (Stahel and Nicol 1982). Two metabolic studies in birds (*Eudiptes chrysolophus chrysolophus* and *Aptenodytes patagonicus*; Barré and Roussel [1986]) and a cooling-constant study in mammals (*S. palustris*, *S. cinereus*, *Z. princeps*, and *P. maniculatus*; Calder [1969]) show a similar magnitude of an approximately fivefold increase of C during diving with minimal compression compared with the C in air as found in the present study (table 2). This might suggest that the order of magnitude of increase of C due to water contact is a rather general phenomenon during swimming and diving.

Several factors increase the C in water, such as motion of the water, motion in water by animals, and compression of the plumage during diving. Two studies show the considerable importance that these factors might have in thermoregulation. Beginning with motion in water by animals, in *Mustela vison* a swimming speed of $0.25 \text{ m} \cdot \text{s}^{-1}$ increases the heat loss by a factor of three compared with the heat loss during resting in water (Williams 1986). With regard to compression, in *Pygoscelis adeliae* a hydrostatic pressure of 2 atm elevates the diving C by 30% (Kooyman et al. 1976). Therefore, the mode of feeding (e.g., dabbling or pursuit diving) and side selection (e.g., swamps or torrents) of species are also important factors in their C 's and their thermoregulatory costs.

Fat has no clear relationship with C in the birds of the present study. We suggest that the subcutaneous fat deposits of our birds are too thin (0.64 cm in *Podiceps cristatus*; Piersma [1984]) to allow a temperature gradient

TABLE 4
Dry C's in various aquatic birds in the air

Species	m (kg)	C (kJ • °C ⁻¹ • h ⁻¹ • kg ⁻¹)					Reference
		Predicted		Measured/Predicted			
		Measured	Herreid and Kessel (1967)	Present Study	Herreid and Kessel (1967)	Present Study	
<i>Clangula hyemalis</i>	.490	.76	.69	.99	1.09	.76	Jenssen and Ekker (1989)
<i>Aythya marila</i>	.59-.80	.58	.63-.53	.84-.78	1.09	.76	McEwan and Koelink (1973)
<i>Anas barbariae</i>	.752	.82	.55	.81	1.49	1.01	Barre et al. (1985)
<i>Anas rubripes</i>	.904	.59	.50	.74	1.18	.80	Hartung (1967)
<i>Eudiptula minor</i>	.900	.62	.50	.75	1.24	.80	Stahel and Nicol (1982)

<i>Anas platyrhynchos</i>	1.263	.49	.42	.63	1.17	.78	Hartung (1967)
<i>Somateria mollissima</i> . . .	1.650	.27	.36	.56	.75	.48	Jenssen, Ekker, and Bech (1989, 1990)
<i>Spheniscus humboldti</i> . . .	3.870	.28	.23	.38	1.22	.74	Drent and Stonehouse (1971)
<i>Pygoscelis adeliae</i>	4.000	.26	.22	.37	1.18	.70	Chappell and Souza (1988)
<i>Anser anser</i>	5.000	.37	.20	.33	1.85	1.11	Bennedict and Lee (1937)
<i>Cygnus olor</i>	8.300	.29	.15	.26	1.90	1.10	Bech (1980)
<i>Aptenodytes fosteri</i>	24.800	.17	.08	.16	2.01	1.08	Le Maho, Delclitte, and Chantonnet (1976)

Note. Predicted values and measured/predicted values are obtained with either the regression of Herreid and Kessel (1967; $C = 0.322m^{-0.484}$) or the regression for species examined in this study ($C = 0.705m^{-0.461}$).

Fig. 3. Comparison between dry C data. The filled circles and the line labeled D & S refer to the regression of the compilation of data obtained by Drent and Stonehouse (1971): $C = 0.430m^{-0.479}$ (C in $\text{kJ} \cdot ^\circ\text{C}^{-1} \cdot \text{h}^{-1} \cdot \text{kg}^{-1}$; m in kg). The line labeled H & K refers to the regression of the cooling constant technique (Herreid and Kessel 1967): $C = 0.474m^{-0.536}$. The line labeled AQUATIC BIRDS refers to the warming constant technique of present study: $C = 0.705m^{-0.461}$. The filled squares refer to gas exchange studies of single species: mute swan (*Cygnus olor*; Bech [1980]), domestic goose (*Anser anser*; Bennedict and Lee [1937]), little penguin (*Eudyptula minor*; Stabel and Nicol [1982]), emperor penguin (*Aptenodytes fosteri*; Le Maho et al. [1976]), and domestic hen (*Gallus gallus*; Romijn and Lokhorst [1966]).

to develop that reduces the heat exchange to the surroundings as in seals and whales (i.e., in seals, 5 cm or more; Irving and Hart [1957]). We are not saying that fat does not act as an insulator, but we stress that it only becomes effective in reducing thermoregulatory costs when the fat layer is thick enough. Irving and Hart (1957) showed that a fat layer becomes an effective insulator when it is approximately 5 cm thick. In birds, fat might therefore be more significant as an energy resource during periods of food deprivation and also when thermoregulatory costs are high.

Age and sex had no apparent effect on C in the birds of the present study. Both between and within species, m has a clear effect on C in air and water. However, in most waterfowl species m is related to sex and age. Therefore, only an indirect influence by sex and age occurs. The generally smaller male

and female juveniles and adult females experience a greater heat loss per unit of m than do the larger adult males.

Intrinsic species characteristics may also further influence the level of C . Although the differences between the slopes of the regression lines for the benthivore *Aythya* and the piscivore *Podiceps* are not significant, they suggest that species characteristics linked with their way of feeding might have an effect on C . The pelagic fish-eating species in figure 1 (b, g, i, j, k, n) have a higher C than the benthic feeders and terrestrial herbivores. We suggest that the pursuit diving technique of fish-eating species might be linked with some adverse effect on C in the same way that we suggested it is between land and aquatic birds.

The explanation for how different-sized aquatic bird species may live in the same wintering area is not found in adaptations of their C 's. The study of Goudie and Ankney (1986) with wintering sea-diving ducks showed that adjustments in behavior and energy content of diets are involved to compensate for the thermodynamic differences associated with body size. The smaller *C. hyemalis* and *Histrionicus histrionicus* spent more time feeding and consumed food items with higher energy content than did the larger *Melanitta nigra* and *S. mollissima* wintering in the same area. But the smaller species were less capable of adjusting their time allocated to feeding to factors increasing energy expenditure such as tide level, wind speed, wind direction, and air temperature. This could become critical to survival of these diurnal feeders during periods of severe winter weather or ice conditions (Goudie and Ankney 1986). A small m in combination with a decreased flexibility in adjusting with feeding to increased energy requirements raises the question of how these two factors are related and if leaving the water might be an attractive behavioral option in this process, because C in air is significantly lower than in water.

We tried to solve these questions by visualizing these factors in a simple model that relates m , air and water temperature, time allocation of water contact, and the energetic costs of thermoregulation (fig. 4). The product of C (in the present study) and difference between T_a and T_b subtracted by the value of basal metabolic rate (BMR) during the resting phase (σ) (Aschoff and Pohl 1970) gave us the cost of thermoregulation. For all m 's we assumed a T_b of 39°C. In figure 4 the isographs of the costs of thermoregulation are expressed in multiples of resting BMR (Aschoff and Pohl 1970). The isographs relate T_a with m for five different levels of costs of thermoregulation. The relationships between m , T_a , and energetic costs of thermoregulation can be summarized as follows from figure 4: decreasing T_a and decreasing m increase thermoregulatory costs; that is,

Fig. 4. Relationship between time allocations in water and on land and the energetic cost of thermoregulation at various temperatures and m 's. The isographs represent the thermoregulatory cost expressed in multiples of the BMR of birds during the resting phase (Aschoff and Pohl 1970).

at the same T_a smaller birds have to spend more energy for thermoregulation than larger birds. The model also indicates that shifts in time allocation in contact with water have a considerable effect on the energetic costs of thermoregulation. In order to cope with the constraints of a higher daily energy expenditure due to thermoregulatory costs, aquatic birds have according to figure 4 three options: (1) to choose sites with high T_a 's, (2) to compensate higher energetic costs of thermoregulation by increasing food intake, and (3) to reduce the energetic costs of thermoregulation by leaving the water.

We will stress the importance of leaving the water as a behavioral adjustment in the corollary of Goudie and Ankney (1986), which explained why different-sized aquatic species may live in the same breeding and/or wintering area. We predict that smaller birds or birds with a diet of low energy content tend to spend more time on land. By reducing the costs of thermoregulation, birds may reduce feeding time and or accept food with less dense energy. In theory, spending time on land makes an aquatic bird more flexible in adjusting its feeding time to meet increasing energetic requirements, for example, during wintertime. In aquatic birds this flexibility may be of paramount importance on both the breeding and wintering grounds as well as in deciding when and where to go during migration.

Acknowledgments

We are grateful to Jan Muller for collecting the birds, to Theun Lindeboom for providing an optimal working place, to Dr. C. Bech and Professor R. H. Drent for their constructive comments on the manuscript, to Dick Visser for preparing the figures, and to Mrs. A. Keyser for correcting the English.

Appendix

TABLE A1
Sample sizes of species obtained and used for C and fat determinations

Species	Age, Sex ^a	Obtained	Used				Fat
			Standing	Swimming	Diving		
<i>Podiceps cristatus</i>	J, M	4	4	4	1	4	
<i>Aythya fuligula</i>	J, M	1	1	1	1	1	
<i>Fulica atra</i>	J, M	1	1	0	0	0	
<i>Mergus serrator</i>	J, M	1	1	1	0	1	
<i>Mergus albellus</i>	J, M	1	1	1	0	1	
<i>Aythya marila</i>	J, M	1	1	1	0	1	
<i>Anas crecca</i>	J, M	1	1	1	1	1	
<i>Somateria mollissima</i> . . .	J, F	1	1	1	1	1	
<i>P. cristatus</i>	J, F	5	4	4	4	5	
<i>A. fuligula</i>	J, F	5	5	5	1	4	
<i>M. albellus</i>	J, F	3	3	2	0	3	
<i>Gavia stellata</i>	J, F	1	1	1	1	1	
<i>A. crecca</i>	J, F	1	1	1	1	1	
<i>Phalacrocorax carbo</i>	A, M	1	1	1	0	1	
<i>Bucephala clangula</i>	A, M	1	1	1	1	1	

<i>P. cristatus</i>	A, M	9	9	9	6	9
<i>Anser anser</i>	A, M	2	2	2	0	2
<i>Mergus merganser</i>	A, M	1	1	1	1	1
<i>A. fuligula</i>	A, M	27	27	26	10	25
<i>M. serrator</i>	A, M	4	4	4	0	3
<i>M. albellus</i>	A, M	2	2	2	1	2
<i>A. marila</i>	A, M	6	6	6	5	5
<i>Anas platyrhynchos</i>	A, M	2	2	2	1	1
<i>A. crecca</i>	A, M	1	1	1	1	1
<i>B. clangula</i>	A, F	4	4	4	1	4
<i>P. cristatus</i>	A, F	3	3	2	2	3
<i>A. anser</i>	A, F	1	1	1	0	1
<i>M. merganser</i>	A, F	1	1	1	0	0
<i>A. fuligula</i>	A, F	7	7	7	2	6
<i>M. albellus</i>	A, F	4	4	2	0	4
<i>A. marila</i>	A, F	7	7	7	4	7
<i>A. crecca</i>	A, F	4	4	4	4	4
Total		113	112	106	50	104

^a J = juvenile, A = adult, M = male, and F = female.

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