

Table 2. Metabolic rates of freely diving birds and mammals.

Species	Family ^a	Mass (kg)	T _w ^b (°C)	Activity ^c	Method ^d	BMR (W)	RMR (W)	MR _d (W)	reference
Birds									
<i>Alle alle</i> (Aal)	Al	0.164	0-5	dfb	DLW		2.2 ^e	8.5	Gabrielsen & Mehlum 1989
<i>Cephus grylle</i> (Cg)	Al	0.381	0-5	dfb	DLW		3.4 ^e	10.0	Gabrielsen & Mehlum 1989
<i>Aythya affinis</i> (Aaf)	An	0.591	12	df	VO ₂		4.8	12.7	Stephenson 1994
<i>Aythya fuligula</i> (Af)	An	0.597	13.6	df	VO ₂	2.9	3.3	10.7	Woakes & Butler 1983, Daan <i>et al.</i> 1990
		0.578	23	df	VO ₂	2.8	3.5	8.0	Bevan & Butler 1992, Daan <i>et al.</i> 1990
		0.605	7.4	df	VO ₂		6.7	11.4	Bevan & Butler 1992
		0.600	22	df	VO ₂	2.9	3.5	11.4	This study, Daan <i>et al.</i> 1990
		0.600	8	df	VO ₂	2.9	5.0	14.7	This study, Daan <i>et al.</i> 1990
<i>Uria lomvia</i> (Ul)	Al	0.803	20	df	VO ₂	5.1	10.6	17	Croll & McLaren 1993, Gabrielsen & Mehlum 1989
<i>Uria aalge</i> (Ua)	Al	0.836	20	df	VO ₂	3.6	8.8	13.8	Croll & McLaren 1993, Cairns <i>et al.</i> 1990
<i>Eudyptula minor</i> (Em)	Sp	1.05	12	df	DLW	4.1	7.0 ^e	22	Gales & Green 1990, Gales <i>et al.</i> 1990
		1.05	16	dfb	DLW	4.1	8.0 ^e	36.8	Gales & Green 1990
		1.094	15	dfb	DLW	4.5	7.1 ^e	14.2	Costa <i>et al.</i> 1986
		1.2	21	ss	VO ₂	4.9	7.7	10.1	Baudinette & Gill 1985
<i>Phalacrocorax carbo</i> (Pc)	Pha	2.4	12.6	ss	VO ₂	7.5	33.8	74.7	Schmid <i>et al.</i> 1995
<i>Eudyptes chrysolophus</i> (Ec)	Sp	3.9	0-5	dfb	DLW	14.8		86.6	Davis <i>et al.</i> 1989, Croxall & Davis 1990
<i>Spheniscus demersus</i> (Sd)	Sp	3.17	15-20	dfb	DLW		13.9 ^e	57.4	Nagy <i>et al.</i> 1984
<i>Spheniscus humboldti</i> (Sh)	Sp	3.78	19.2	ss	VO ₂	9.3	27.2	55.8	Hui 1988, Drent & Stonehouse 1970
		4.6	18	di	VO ₂	11.3	20.0	37.5	Butler & Woakes 1984
<i>Pygoscelis antarctica</i> (Pan)	Sp	3.8	4	ss	VO ₂	14.1	33.3	33.8	Culik <i>et al.</i> 1994, Croxall & Davis 1990
<i>Pygoscelis adeliae</i> (Pad)	Sp	4	4	ss	VO ₂	14.8	33.6	43.2	Culik <i>et al.</i> 1994, Croxall & Davis 1990
		4.1	0-5	dfb	DLW	12.5		60	Green & Gales 1990
		4.2	0-5	df	DLW	12.8		55.9	Culik & Wilson 1992
<i>Pygoscelis papua</i> (Pp)	Sp	5.5	4	ss	VO ₂	20.4	45.1	75.4	Culik <i>et al.</i> 1994
		6.1	0-5	dfb	DLW			97	Davis <i>et al.</i> 1989
<i>Aptenodytes patagonicus</i> (Ap)	Sp	13	0-5	df	DLW			79.3	Kooyman <i>et al.</i> 1982
		16.2	0-5	dfb	DLW	40.5	68	161	Kooyman <i>et al.</i> 1992a
		11.5	9.1	ss	VO ₂		13.5	96.6	Culik <i>et al.</i> 1996
Mammals									
<i>Mustela vison</i> (Mv)	Mu	0.825		da	VO ₂			29	Stephenson <i>et al.</i> 1988
<i>Ondatra zibethicus</i> (Oz)	Mi	0.861	3	da	VO ₂	3.8	3.9 ^e	11.4	MacArthur 1984
		0.861	30	da	VO ₂	3.8	3.8 ^e	6.2	MacArthur 1984
		0.932	18.5	da	VO ₂	4.2		10.2	MacArthur & Campbell 1994
		1.001	29.5	da	VO ₂	4.4	4.5	8.3	MacArthur & Krause 1989
<i>Enhydra lutris</i> (El)	Mu	19.9	18	ss	VO ₂		91.1	118.4	Williams 1989
<i>Zalophus californianus</i> (Zc)	Ot	20.2	22	ss	VO ₂		49.4	131	Feldkamp 1987, Feldkamp <i>et al.</i> 1989
		21	16.5	ss	VO ₂			115	Williams <i>et al.</i> 1991
<i>Arctocepalus gazella</i> (Ag)	Ot	31.5	0-5	dfb	DLW		156 ^e	300	Costa <i>et al.</i> 1989, Boyd <i>et al.</i> 1994
<i>Callorhinus ursinus</i> (Cu)	Ot	44	5-10	dfb	DLW	146	203 ^e	365	Costa & Gentry 1986
<i>Phoca vitulina</i> (Pv)	Pho	32	16.5	ss	VO ₂			199	Williams <i>et al.</i> 1991
		42.5	18	di	VO ₂		105	142	Craig & Päsche 1980
		33	16.5	ss	VO ₂	40	56	146	Davis <i>et al.</i> 1985
		63	16.5	ss	VO	271	97	182	Davis <i>et al.</i> 1985
		100	10-15	df	DLW	106		602	Reilly & Fedak 1991
<i>Phoca groenlandica</i> (Pg)	Pho	162		di	VO ₂			200	Gallivan 1981
<i>Halochoerus grypus</i> (Hg)	Pho	160	15-20	di	VO ₂	159		275	Reed <i>et al.</i> 1994
		180	10-15	ss	VO ₂	194	201	975	Fedak <i>et al.</i> 1988
<i>Leptonychotes weddelli</i> (Lw)	Pho	150	-2	da	VO ₂		322 ^f	352	Ponganis <i>et al.</i> 1993
		355	-2	df	VO ₂	416	488 ^f	595	Castellini <i>et al.</i> 1992
		355	-2	di	VO ₂	416	488 ^f	404	Castellini <i>et al.</i> 1992
		425	-2	da	VO ₂		733 ^f	603	Kooyman <i>et al.</i> 1973
<i>Balaenoptera acutorostrata</i> (Ba)Ba		4000	0-5	df	RF			4197	Blix & Folkow 1995, Folkow & Blix 1992
		4000	5-10	dt	RF			3466	Blix & Folkow 1995
<i>Eschrichtius robustus</i> (Er)	Es	15000	10-15	dt	RF			13958	Sumich 1983
<i>Megaptera novaeangliae</i> (Mn)	Ba	32700	5-10	df	RF		51200	79300	Dolphin 1987

a) Family: Al = Alcidae (auks), An = Anatidae (waterfowl), Pha = Phalacrocoracidae (cormorants), Sp = Spheniscidae (penguins), Mu = Mustelidae (marters), Mi = Microtidae (voles), Ot = Otariidae (fur seals and sea lions), Pho = Phocidae (seals), Ba = Balaenopteridae, Es = Eschrichtiidae (whales)

b) Water temperature, 5 °C temperature classes from Couper (1983)

c) Activity: di = inactive dives, da = active dives, df = feeding dives, dfb = feeding dives in breeding season, dt = dives at slow travel speeds, ss = subsurface swimming

d) Method: VO₂ = oxygen consumption by respirometry, DLW = doubly labelled or tritiated water, RF = respiratory frequency

e) resting on land

f) sleeping dives

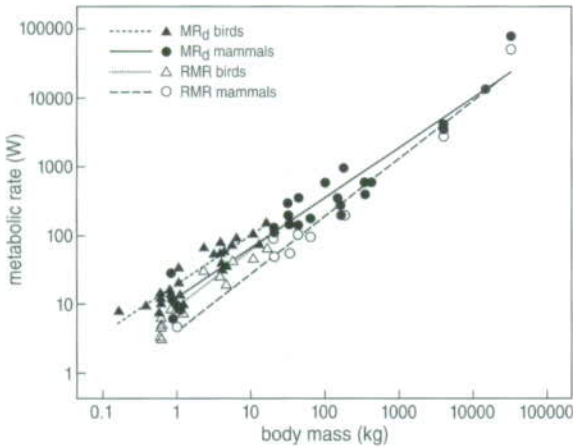


Fig. 4. Allometric relations of diving metabolic rate (MR_d) and resting on the water (RMR) in birds and mammals.

(Butler & Jones 1982, Kooyman 1989). Studies using animals with external instrumentation were excluded, since such devices increase hydrodynamic drag (e.g., Culik & Wilson 1992). A variety of methods have been used, both in the laboratory and in the field, to estimate diving costs. In most laboratory studies, animals were diving freely in a tank and could breathe under a dome where gas exchange was measured (VO_2). For

penguins and larger sea mammals that swim actively while diving, the oxygen consumption of animals swimming submerged in a water flume at optimal swimming speed (i.e. at minimal cost of transport, which is usually equivalent to preferred swimming speeds observed in the field) or swimming at their preferred speed in a swim canal were used. Swimming speeds that deviated by more than 20% from the average swimming speed observed in the field were excluded from the analyses. In studies using a swim canal, only values corrected for deceleration and acceleration were used (Culik *et al.* 1994). Field studies using the tritiated or doubly labelled water technique (DLW) in penguins and mammals making foraging trips at sea and swimming underwater and diving to depth for most of their time at sea were also included in the analyses. Since resting periods at sea were short in the selected studies, these measurements probably do not underestimate diving metabolism as argued by Wilson & Culik (1993). Because of their large size, conventional methods are not applicable to whales, but diving metabolism in these animals could be assessed from their respiratory frequencies observed in the field (Dolphin 1987, Sumich 1983, Blix & Folkow 1995). Folkow & Blix (1992) measured respiratory tidal volume and oxygen extraction in Minke Whales *Bal-*

Table 3. Linear equations for \log_{10} - \log_{10} regressions of diving (MR_d) and resting (RMR) metabolic rates (W) against body mass (kg) from least-squares regressions and ANCOVA using common slopes for the data presented in Table 2. Values in parentheses are standard errors.

	Intercept	Slope	n	r^2	P
All birds and mammals diving	1.24 (0.04)	0.676 (0.024)	54	0.94	< 0.001
Birds					
Resting on the water	0.90 (0.04)	0.875 (0.076)	17	0.90	< 0.001
Diving	1.28 (0.03)	0.717 (0.059)	28	0.85	< 0.001
Foraging trip at sea	1.36 (0.03)	0.698 (0.930)	12	0.89	< 0.001
Dive bout	1.23 (0.03)	0.698 (0.930)	16	0.89	< 0.001
Mammals					
Resting on the water	0.59 (0.12)	0.838 (0.048)	13	0.97	< 0.001
Diving	1.07 (0.08)	0.731 (0.038)	26	0.94	< 0.001
Foraging trip at sea	1.35 (0.09)	0.734 (0.975)	3	0.96	< 0.001
Dive bout	1.03 (0.07)	0.734 (0.975)	23	0.96	< 0.001
Inactive dives	0.80 (0.07)	0.732 (0.985)	4	0.98	< 0.001
Low-speed travel or moderate activity	0.96 (0.06)	0.732 (0.985)	8	0.98	< 0.001
Feeding dives or submerged swimming	1.17 (0.07)	0.732 (0.985)	11	0.98	< 0.001

probably as a result of the difference in time-frame of the measurements (see below).

Dive duration is strongly related to diving depth in most animals. The effect of dive duration or diving depth on energy costs has rarely been studied, since most laboratory studies are confined to a single depth, and in the field, diving depths are variable and are usually not measured simultaneously with energy costs. In the Emperor Penguin *Aptenodytes forsteri* (Kooyman *et al.* 1992b), Weddell Seal (Castellini *et al.* 1992), and Tufted Duck (Woakes & Butler 1983, Bevan *et al.* 1992), heart rate and oxygen consumption were reported to be lower during dives of longer duration. However, these measurements refer only to the short intervals between dives or are extrapolated values for metabolism during the underwater phase of the dive. Possible effects of greater cooling (Tufted Duck and Weddell Seal) and (or) an increased reliance on anaerobic metabolism (Weddell Seal study; Kooyman *et al.* 1980) in dives of long duration and, consequently, more costly recoveries were not included. Moreover, Weddell Seals engaged in exploratory dives of long duration were less active than animals involved in short dives for hunting or social and antagonistic behaviour, which incurred higher hydromechanical diving costs.

Levels of diving activity in the literature were classified as low (inactive dives), moderate (active dives and travelling at low speed), and high (submerged swimming and feeding dives). Diving metabolic rates of mammals increased with the level of activity (ANCOVA, $F_{2,22} = 10.4$, $P = 0.001$, Table 3). In birds, activity was usually high during diving, but in the study by Butler & Woakes (1984), the metabolic rate of an almost motionless diving Humboldt's Penguin *Spheniscus humboldti* was considerably lower than in actively diving birds (Hui 1988). The equations for birds compare well with the equation derived by Birt-Friesen *et al.* (1989) for seabirds engaged in flapping flight or pursuit diving (Fig. 5). As mentioned earlier, diving is a costly activity in birds, owing to the high costs they incur to overcome buoyancy.

Incorporating diving costs into time and energy budgets

The consequence of the large differences in diving costs among species for their daily time budgets is il-

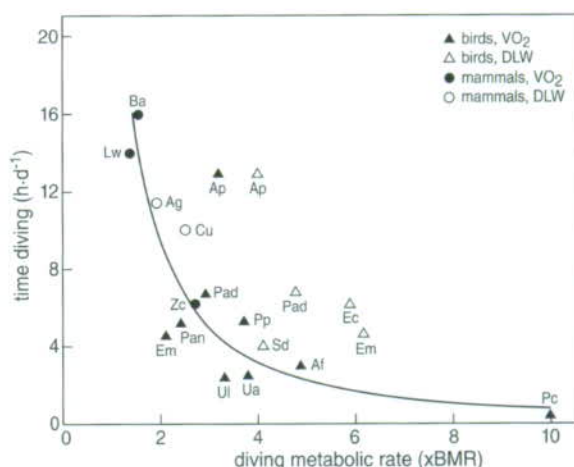


Fig. 6. Relationship between daily diving activity and MR_d (expressed as a multiple of BMR). For references see Table 2; Af: Suter (1982); Pc: Platteeuw & Van Eerden (1995); Voslamber *et al.* (1995); Ua: Monaghan *et al.* (1994); Ul: Croll *et al.* (1992); Ag: Gentry *et al.* (1986). For an explanation of abbreviations see Table 2.

lustrated in Fig. 6. The maximum daily time spent in diving and subsurface travelling observed in field studies is negatively related to MR_d (as a multiple of BMR) (regression of \log_{10} - \log_{10} transformed data: $r^2 = 0.75$, $P < 0.001$ for VO_2 studies; excluding the cormorant study (Pc), $P = 0.003$; DLW data were significantly higher: ANCOVA, $F_{1,16} = 9.9$, $P = 0.006$; see references in Table 2 and Fig. 6). Although the maximum daily dive time is hard to determine from the few studies reporting time budgets, the inverse relationship suggests that animals coping with high diving costs, like many birds, can spend less time diving per day than, for example, the large sea mammals, which enjoy low diving costs. These animals live most of their time underwater and have been classified as 'surfacers' rather than 'divers' (Kramer 1988, Kooyman 1989). At the other extreme, owing to the poor insulation provided by its wet plumage while diving, the Cormorant *Phalacrocorax carbo* can remain submerged for only short periods and must rest on land to recover from heat loss (Schmid *et al.* 1995). If longer term recovery costs were included, the relationship between diving cost and time budgets might be even stronger.

To assess the contribution of diving costs to the energy budget of animals, it is convenient to express div-

Table 4. Energy investment ($J \cdot s^{-1}$) calculated from mean MR_d and percentage of time spent diving during the dive cycle (estimated EDC) and directly measured EDC.

Species	T_w	estimated EDC	measured EDC	Reference
<i>Aythya fuligula</i>	8	19	43	This study
	22	16	23	This study
<i>Ondatra zibethicus</i>	3	39.4	86.0	MacArthur 1984 ^a
	30	16.1	23.1	MacArthur 1984 ^a
	30	5.9	10.7	MacArthur & Krause 1989 ^b

^a) Includes grooming activity (animals left the water after diving).

^b) No grooming activity (animals remained in the water).

ing costs as the excess over resting costs. If full recovery from diving takes place within the dive cycle, EDC (energy expenditure in excess of the resting rate per second spent underwater) can be estimated from the difference between MR_d and RMR divided by the proportion of time spent diving during a dive cycle. However, if full recovery from diving is postponed until after a dive bout, the time frame over which MR_d is measured would be too short and EDC would be underestimated using MR_d values. Three studies confined to Tufted Ducks and Muskrats enable us to make a comparison between the estimated EDC using MR_d measurements and the directly measured EDC of a dive bout (Table 4). In all cases the measured EDC is considerably higher than the EDC estimated from MR_d . Moreover, at lower temperatures the differences are larger, demonstrating again that MR_d may be a poor estimate of the increase in thermoregulatory costs due to diving in these small endothermic divers. In the comparative analyses there was no significant effect of water temperature on MR_d despite the large range in temperatures (ANCOVA, with water temperature (< 10, 10–20, and > 20 °C), method, activity, and bird or mammal as factors and the logarithm of body mass as covariate, $F_{2,39} = 1.32$, $P = 0.28$). Owing to their high ratio of surface area to body volume, small animals are more sensitive to heat loss than large animals, but even in animals as large as a 400 kg Weddell Seal (Kooyman *et al.* 1980), a drop in body temperature after long dives in cold water has been recorded. In general, the thermoregulatory component of diving costs seems to be underestimated in metabolic studies.

The analysis of data in the literature revealed that

the metabolic rate of diving animals during entire foraging trips (DLW measurements) was higher, on average, than when it was measured during diving activity only (VO_2), even for the most active divers (Fig. 5). Culik *et al.* (1994) mentioned that travel to and from foraging sites is more costly than foraging dives in Adélie Penguins, owing to higher swimming speeds. This suggests that subsurface swimming measurements would rather overestimate the costs of a foraging trip. Taking into account that the foraging trip studies did not control for resting periods at sea (though these were short in the selected studies), it is conceivable that the higher costs measured during the foraging trip studies reflect extra energy costs for feeding and digestion and for recovery from heat loss or anaerobic metabolism that may be covered after the diving bouts. These costs become apparent in the foraging trip studies because the time frame of measurement is longer than in the diving activity studies. Although DLW measurements include longer term recovery costs, problems may arise when the technique is applied to estimating activity-specific metabolism (Wilson & Culik 1993). Also, the technique may affect the behaviour of the animals under study (e.g., Wilson & Culik 1995). Heart rate measurements have been proposed as an alternative method to study diving energetics in sea lions (Butler *et al.* 1992) and Tufted Ducks (Bevan *et al.* 1995).

The large difference between the metabolic rates obtained from foraging trip studies and from studies confined within dive bouts and the direct comparison of EDC and MR_d estimates (Table 4) suggests that measurements within dive bouts generally underesti-

mate the energy costs incurred during diving. This holds particularly for small animals sensitive to heat loss and animals relying on anaerobic metabolism during dives of long duration. Future studies taking into account the costs of recovery after a dive bout would greatly enhance our knowledge concerning the importance of diving costs to an animal's energy budget.

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References

- Bartholomew, G.A., Vleck, D. & Vleck, C.M. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in *Sphingid* and *Saturniid* moths. *J. Exp. Biol.* 90: 17-32.
- Baudinette, R.V. & Gill, P. 1985. The energetics of flying and paddling in water: locomotion in penguins and ducks. *J. Comp. Physiol. A* 155: 373-380.
- Bevan, R.M. & Butler, P.J. 1992. The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the Tufted Duck (*Aythya fuligula*). *J. Exp. Biol.* 163: 139-151.
- Bevan, R.M., Speakman, J.R. & Butler, P.J. 1995. Daily energy expenditure of Tufted Ducks: a comparison between indirect calorimetry, doubly labelled water and heart rate. *Funct. Ecol.* 9: 40-47.
- Birt-Friesen, V.L., Montevecchi, W.A., Cairns, D.K. & Macko, S.A. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other sea-birds. *Ecology* 70: 357-367.
- Blix, A.S. & Folkow, L.P. 1995. Daily energy expenditure in free living Minke Whales. *Acta Physiol. Scand.* 153: 61-66.
- Boyd, I.L., Arnould, J.P.Y., Barton, T. & Croxall, J.P. 1994. Foraging behavior of Antarctic Fur Seals during periods of contrasting prey abundance. *J. Anim. Ecol.* 63: 703-713.
- Butler, P.J. & Jones, D.R. 1982. The comparative physiology of diving in vertebrates. *Adv. Comp. Physiol. Biochem.* 8: 179-364.
- Butler, P.J. & Woakes, A.J. 1984. Heart rate and aerobic metabolism in Humboldt Penguins *Spheniscus humboldti* during voluntary dives. *J. Exp. Biol.* 108: 419-428.
- Butler, P.J., Woakes, A.J., Boyd, I.L. & Kanatous, S. 1992. Relationship between heart rate and oxygen consumption during steady-state swimming in California Sea Lions. *J. Exp. Biol.* 170: 35-42.
- Cairns, D.K., Montevecchi, W.A., Birt-Friesen, V.L. & Macko, S.A. 1990. Energy expenditures, activity budgets, and prey harvest of breeding Common Murres. *Studies in Avian Biol.* 14: 84-92.
- Carbone, C., de Leeuw, J.J. & Houston, A.I. 1996. Adjustments in the diving time budgets of Tufted Duck and Pochard: is there evidence for a mix of metabolic pathways? *Anim. Behav.* 51: 1257-1268.
- Castellini, M.A., Murphy, B.J., Fedak, M.A., Ronald, K., Gofton, N. & Hochachka, P.W. 1985. Potentially conflicting metabolic demands of diving and exercise in seals. *J. Appl. Physiol.* 58: 392-399.
- Castellini, M.A., Kooyman, G.L. & Ponganis, P.J. 1992. Metabolic rates of freely diving Weddell Seals: correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* 165: 181-194.
- Costa, D.P., Dann, P. & Disher, W. 1986. Energy requirements of free-ranging Little Penguin *Eudyptula minor*. *Comp. Biochem. Physiol. A* 85: 135-138.
- Costa, D.P. 1988. Methods for studying the energetics of freely diving animals. *Can. J. Zool.* 66: 45-52.
- Costa, D.P., Croxall, J.P. & Duck, C.D. 1989. Foraging energetics of Antarctic Fur Seals in relation to changes in prey availability. *Ecology* 70: 596-606.
- Costa, D.P. & Gentry, R.L. 1986. Free-ranging energetics of Northern Fur Seals. In: R.L. Gentry & G.L. Kooyman (Eds). *Fur Seals. Maternal strategies on land and sea*. Princeton University Press, Princeton, pp. 79-101.
- Costa, D.P. & Kooyman, G.L. 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the Sea Otter *Enhydra lutris*. *Physiol. Zool.* 57: 199-203.
- Couper, A. 1983. *Times Atlas of the Oceans*. Times Books, London.
- Craig, A.B. & Päsche, A. 1980. Respiratory physiology of freely diving Harbor Seals *Phoca vitulina*. *Physiol. Zool.* 53: 419-432.
- Croll, D.A. & McLaren, E. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. *J. Comp. Physiol. A* 163: 160-166.
- Croll, D.A., Gaston, A.J., Burger, A.E. & Konnoff, D. 1992. Foraging behaviour and physiological adaptation for diving in Thick-billed Murres. *Ecology* 73: 344-356.
- Croxall, J.P. & Davis, R.W. 1990. Metabolic rate and foraging behaviour of *Pygoscelis* and *Eudyptes* penguins at sea. In: L.S.

- Davis & J.T. Darby (Eds). Penguin Biology. Academic Press, San Diego, pp. 207-228.
- Culik, B.M., Pütz, K., Wilson, R.P., Allers, D., Lage, J., Bost, C.A. & Le Maho, Y. 1996. Diving energetics in King Penguins *Aptenodytes patagonicus*. J. Exp. Biol. 199: 973-983.
- Culik, B.M., Wilson, R.P. & Bannasch, R. 1994. Underwater swimming at low energetic cost by *Pygoscelis* penguins. J. Exp. Biol. 197: 65-78.
- Culik, B.M. & Wilson, R.P. 1992. Field metabolic rates of instrumented Adélie Penguins using double-labelled water. J. Comp. Physiol. A 162: 567-573.
- Daan, S., Masman, D. & Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. 259: R333-R340.
- Davis, R.W., Williams, T.M. & Kooyman, G.L. 1985. Swimming metabolism of yearling and adult Harbor Seals *Phoca vitulina*. Physiol. Zool. 58: 590-596.
- Davis, R.W., Croxall, J.P. & O'Connell, M.J. 1989. The reproductive energetics of Gentoo *Pygoscelis papua* and Macaroni *Eudyptes chrysolophus* Penguins at South Georgia. J. Anim. Ecol. 58: 59-74.
- 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. Physiol. Zool. 68: 1143-1163.
- Dolphin, W.F. 1987. Dive behavior and estimated energy expenditure of foraging Humpback Whales in southeast Alaska. Can. J. Zool. 65: 354-362.
- Drent, R.H. & Stonehouse, B. 1971. Thermoregulatory responses of the Peruvian Penguin *Spheniscus humboldti*. Comp. Biochem. Physiol. A 40: 689-710.
- Fedak, M.A., Pullen, M.R. & Kanwisher, J. 1988. Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. Can. J. Zool. 66: 53-60.
- Feldkamp, S.D. 1987. Swimming in the California Sea Lion: morphometrics, drag and energetics. J. Exp. Biol. 131: 117-135.
- Feldkamp, S.D., DeLong, R.L. & Antonelis, G.A. 1989. Diving patterns of California Sea Lions *Zalophus californianus*. Can. J. Zool. 67: 872-883.
- Folkow, L.P. & Blix, A.S. 1992. Metabolic rates of Minke Whales *Balaenoptera acutorostrata* in cold water. Acta Physiol. Scand. 146: 141-150.
- Gabrielsen, G.W. & Mehlum, F. 1989. Thermoregulation and energetics of arctic seabirds. In: C. Bech & R.E. Reinertsen (Eds). Physiology of cold adaptation in birds. Plenum, New York, pp. 137-145.
- Gales, R.P., Williams, C. & Ritz, D. 1990. Foraging behaviour of the little penguin *Eudyptula minor*: initial results and assessment of instrument effect. J. Zool. Lond. 220: 61-85.
- Gales, R.P. & Green, B. 1990. The annual energetics cycle of Little Penguins *Eudyptula minor*. Ecology 71: 2297-2312.
- Gallivan, G.J. 1981. Ventilation and gas exchange in unrestrained Harp Seals *Phoca groenlandica*. Comp. Biochem. Physiol. A 69: 809-813.
- Gentry, R.L., Kooyman, G.L. & Goebel, M.E. 1986. Feeding and diving behavior of Northern Fur Seals. In: R.L. Gentry & G.L. Kooyman (Eds). Fur seals: maternal strategies on land and at sea. Princeton Univ Press, New Jersey, pp 61-78.
- Green, B. & Gales, R.P. 1990. Water, sodium, and energy turnover in free-living penguins. In: L.S. Davis & J.T. Darby (Eds). Penguin Biology. Academic Press, San Diego, pp. 245-268.
- Hui, C.A. 1988. Penguin swimming. II. Energetics and behaviour. Physiol. Zool. 61: 344-350.
- Keijer, E. & Butler, P.J. 1982. Volumes of the respiratory and circulatory systems in Tufted and Mallard Ducks. J. Exp. Biol. 101: 213-220.
- Kooyman, G.L., Kerem, D.H., Campbell, W.B. & Wright, J.J. 1973. Pulmonary gas exchange in freely diving Weddell Seals *Lep- tonychotes weddelli*. Respir. Physiol. 17: 283-290.
- Kooyman, G.L., Gentry, R.L., Bergman, W.P. & Hammel, H.T. 1976. Heat loss in penguins during immersion and compression. Comp. Biochem. Physiol. A 54: 75-80.
- Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W. & Sinnett, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell Seals: evidence of preferred pathways from blood chemistry and behavior. J. Comp. Physiol. A 138: 335-346.
- Kooyman, G.L., Davis, R.W., Croxall, J.P. & Costa, D.P. 1982. Diving depths and energy requirements of King Penguins. Science 217: 726-727.
- Kooyman, G.L. 1989. Diverse Divers. Physiology and behavior. Springer-Verlag, Berlin.
- Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V. & Kooyman, C.A. 1992. Diving behaviour and energetics during foraging cycles in King Penguins. Ecolog. Monogr. 62: 143-163.
- Kooyman, G.L., Ponganis, P.J., Castellini, M.A., Ponganis, E.P., Ponganis, K.V., Thorson, P.H., Eckert, S.A. & Le Maho, Y. 1992. Heart rates and swim speeds of Emperor Penguins diving under sea ice. J. Exp. Biol. 165: 161-180.
- Kramer, D.L. 1988. The behavioural ecology of air breathing in aquatic animals. Can. J. Zool. 66: 89-94.
- Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J. & Hickie, J.P. 1986. Metabolic rates of seals and whales. Can. J. Zool. 64: 279-284.
- Lovvorn, J.R. & Jones, D.R. 1991. Effects of body size, body fat, and changes in pressure with depth on buoyancy and costs of diving in ducks *Aythya* spp. Can. J. Zool. 69: 2879-2887.
- Lovvorn, J.R. & Jones, D.R. 1994. Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. Es-

- tuaries 17: 62-75.
- MacArthur, R.A. 1984. Aquatic thermoregulation in the Muskrat *Ondatra zibethicus*: energy demands of swimming and diving. *Can. J. Zool.* 62: 241-248.
- MacArthur, R.A. & Campbell, K.L. 1994. Heat increment of feeding and its thermoregulatory benefit in the Muskrat *Ondatra zibethicus*. *J. Comp. Physiol. A*, 164: 141-146.
- MacArthur, R.A. & Krause, R.E. 1989. Energy requirements of freely diving Muskrats *Ondatra zibethicus*. *Can. J. Zool.* 67: 2194-2200.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. & Burns, M.D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. *Ibis* 136: 214-222.
- Nagy, K.A., Siegfried, W.R. & Wilson, R.P. 1984. Energy utilization by free-ranging Jackass Penguins *Spheniscus demersus*. *Ecology* 65: 1648-1655.
- Platteeuw, M. & Van Eerden, M.R. 1995. Time and energy constraints of fishing behaviour in breeding Cormorants at Lake IJsselmeer, The Netherlands. *Ardea* 83: 223-234.
- Ponganis, P.J., Kooyman, G.L. & Castellini, M.A. 1993. Determinants of the aerobic dive limit of Weddell Seals: analysis of diving metabolic rates, postdive end tidal PO_2 's, and blood and muscle oxygen stores. *Physiol. Zool.* 66: 732-749.
- Reed, J.Z., Chambers, C., Fedak, M.A. & Butler, P.J. 1994. Gas exchange of captive freely diving Grey Seals *Halichoerus grypus*. *J. Exp. Biol.* 191: 1-18.
- Reilly, J.J. & Fedak, M.A. 1991. Rates of water turnover and energy expenditure of free-living male Common Seals *Phoca vitulina*. *J. Zool., Lond.* 23: 461-468.
- Schmid, D., Grémillet, D.J.H. & Culik, B.M. 1995. Energetics of underwater swimming in the Great Cormorant *Phalacrocorax carbo sinensis*. *Mar. Biol.* 123: 875-881.
- Stephenson, R., Butler, P.J., Dunstone, N. & Woakes, A.J. 1988. Heart rate and gas exchange in freely diving American Mink *Mustela vison*. *J. Exp. Biol.* 134: 435-442.
- Stephenson, R. 1994. Diving energetics in Lesser Scaup *Aythya affinis* (Eyton). *J. Exp. Biol.* 190: 155-178.
- Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating Gray Whales *Eschrichtius robustus*. *Can. J. Zool.* 61: 647-652.
- Suter, W. 1982. Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala*, *Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/Hochrhein (Bodensee). *Orn. Beob.* 79: 225-254.
- Voslammer, B., Platteeuw, M. & Van Eerden, M.R. 1995. Solitary foraging in sand pits by breeding Cormorants: does specialised knowledge about fishing sites and fish behaviour pay off? *Ardea* 83: 213-222.
- Williams, T.M. 1989. Swimming by Sea Otters: adaptations for low energetic cost of locomotion. *J. Comp. Physiol. A* 164: 815-824.
- Williams, T.M., Kooyman, G.L. & Croll, D.A. 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. Comp. Physiol. A* 160: 637-644.
- Wilson, R.P. & Culik, B.M. 1993. Activity-specific metabolic rates from doubly labeled water studies: are activity costs underestimated? *Ecology* 74: 1285-1287.
- Wilson, R.P. & Culik, B.M. 1995. Energy studies of free-living seabirds: do injections of doubly-labeled water affect Gentoo Penguin behaviour? *J. Field Ornithol.* 66: 484-491.
- Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E. & Nöldeke, C.E. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am. Nat.* 140: 179-200.
- Woakes, A.J., & Butler, P.J. 1983. Swimming and diving in Tufted Ducks *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* 107: 311-329.

Chapter 6

Body cooling and its energetic implications for feeding and diving of Tufted Ducks

J.J. de Leeuw, P.J. Butler, A.J. Woakes & F. Zegwaard

Submitted



Body cooling and its energetic implications for feeding and diving of Tufted Ducks

Wintering in a temperate climate with low water temperatures is energetically expensive for diving ducks. The energy costs associated with body cooling due to diving and ingesting large amounts of cold food were measured in Tufted Ducks *Aythya fuligula* feeding on Zebra Mussels *Dreissena polymorpha*, using implanted heart rate and body temperature transmitters. The effects of diving depth and food ingestion were measured in two sets of experiments: we measured body cooling and energy costs of six Tufted Ducks diving to different depths in a 6 m deep indoor tank. Secondly, the costs for food ingestion and crushing mussel shells were assessed under semi-natural winter conditions with the same ducks feeding on mussels in a 1.5 m deep outdoor basin. Body temperature dropped during feeding bouts and increased gradually during intermittent resting periods. Body cooling increased with dive duration and diving depth, although the relative cooling was lower again at depths below 4 m. The energy costs in excess of resting costs amounted to 42 J.s^{-1} spent diving. Half of this increment can be attributed to thermoregulatory heat production, of which approximately 50% is generated after diving to warm up the body. The excess costs for ducks feeding on large sized mussels could be entirely explained by the estimated energy cost necessary to compensate the heat loss following food ingestion, suggesting that the heat production from shell crushing substituted for thermoregulation. Recovery from heat loss is probably a major component of the activity budget of wintering diving ducks.

Introduction

Most endotherms regulate their body temperature within narrow margins to optimise their metabolic functions (Blaxter 1989). Body temperature can be controlled by a variety of physiological, anatomical, and behavioural adaptations (McNab 1980, Blaxter 1989). Nevertheless, fluctuations in body temperature of 1–3 °C around normal resting levels are characteristic of birds, owing to, for example, variation in activity over the diurnal cycle (Prinzinger *et al.* 1991) or ingestion of food of considerable lower temperature than the body (Wilson & Culik 1991).

Aquatic birds living in cold environments have to maintain a high body temperature against the considerable cooling properties of water. Therefore, maintenance costs are high for birds resting in water, like diving ducks (Jenssen & Ekker 1989, Jenssen *et al.* 1989, Bevan & Butler 1992a, De Leeuw 1996), guillemots

(Croll & McLaren 1993), and penguins (Kooyman *et al.* 197, Stahel & Nicol 1982). Thermal conductance increases while diving (Kooyman *et al.* 1976, De Vries & Van Eerden 1995), and it is questionable whether body temperature can be maintained during diving when the oxygen supply is limited. Bevan & Butler (1992a) reported that body temperature of Tufted Ducks *Aythya fuligula* was lower after diving in cold water. Also, in Muskrats *Ondatra zibethicus* (MacArthur 1984), and Weddell Seals *Leptonychotes weddelli* (Kooyman *et al.* 1980), body temperature dropped during diving. The metabolic cost associated with body cooling in diving animals is poorly known, because an elevation of metabolism for extra thermoregulation may be postponed until after diving and, therefore, may be difficult to measure (De Leeuw 1996).

The ingestion of food at low temperatures may also contribute considerably to the daily energy expenditure

(DEE) of aquatic birds, for example: 6% of DEE in fish-eating Great Crested Grebes *Podiceps cristatus* in winter (Wiersma *et al.* 1995), and 13–20% in mollusc-feeding Eiders *Somateria mollissima* (Nehls 1995) and Tufted Ducks (De Leeuw *et al.*, in prep.). The contribution of other feeding costs to DEE (costs for food acquisition, food processing, digestion) is not straightforward, because heat generated by these activities may to some extent compensate the obligatory costs for thermoregulation (Wieser 1989). The amount of heat that can be substituted seems to vary between nil and full substitution, probably depending on the thermoregulatory demands of the animal under study (e.g., Kleiber 1961, Pohl & West 1973, Paladino & King 1984, Wilson & Culik 1991, Nehls 1995).

In the small-sized Tufted Duck (body mass less than 1 kg) feeding on Zebra Mussels *Dreissena polymorpha*, the daily energy costs are extremely high, owing to high thermoregulatory costs for living in cold water (De Leeuw *et al.*, in prep.). Diving costs increase at lower water temperatures (De Leeuw 1996), suggesting considerable thermoregulatory costs in addition to hydromechanical costs of overcoming buoyancy and drag while swimming under water (Lovvorn & Jones 1991, Stephenson 1994). To meet their daily energy demands, Tufted Ducks consume large amounts of mussels (up to three times their body mass per day; De Leeuw *et al.*, in prep.). The mussels are ingested whole and the shells are crushed in the muscular gizzard, probably incurring considerable costs for heating up the large cold food mass and for crushing the shells (Nehls 1995).

We studied the impact of diving and food ingestion on maintaining body temperature and the associated energy costs of feeding in Tufted Ducks under cold winter conditions, when thermoregulatory demands are maximal. We used implanted heart rate and body temperature transmitters, which allow the birds to perform their natural diving behaviour, while rapid changes in metabolic rate can be identified. Heart rate has proven to be a good estimate of energy expenditure in diving Tufted Ducks (Woakes & Butler 1983, Bevan & Butler 1992a, Bevan *et al.* 1995). Two sets of experiments were carried out: (1) the costs of body cooling and diving in relation to feeding depth were measured in Tufted Ducks diving in a 5.7 m deep indoor tank, and (2) the costs of feeding on mussels (crushing shells

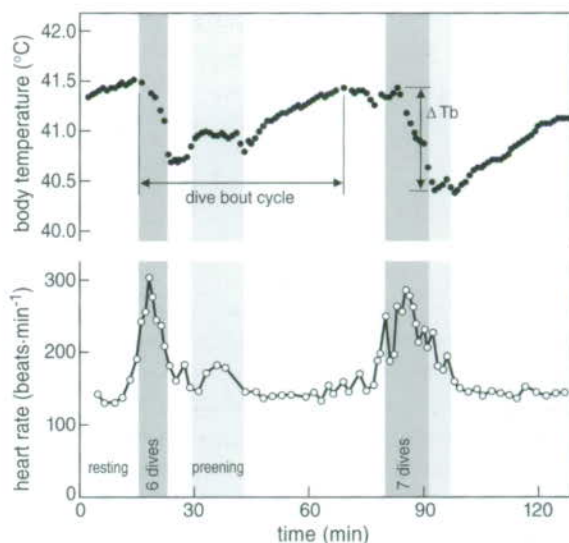


Fig. 1. Illustration of changes in heart rate (1-min. averages) and body temperature of a Tufted Duck diving to 5.5 m. Two dive bouts of 6 and 7 dives, respectively, and preening periods are indicated. ΔT_b is the maximum difference in body temperature before and after diving. The unit for energetic measurements was the dive bout cycle (series of dives plus the subsequent period of body temperature increase).

and the ingestion of cold food masses) were determined under semi-natural conditions in an outdoor 1.5 m deep pond. In particular, we focus on the relevance of heat substitution and recovery from heat loss for time and energy budgets of Tufted Ducks.

Material and Methods

Six Tufted Ducks (four males and two females with mean body masses of 606 ± 42 g) were provided with implantable heart rate and body temperature transmitters under halothane anaesthesia. The transmitters were positioned in the abdominal cavity with electrodes under the sternum close to the heart. A detailed description of the operation procedures is given in Stephenson *et al.* (1986). The ECG signal of the transmitter was recorded via a radio receiver and a purpose-built decoder on tape recorder or videorecorder for later analysis. The temperature modulated frequency of the signal was used to determine body temperature

in the abdominal cavity (accurate to 0.05 °C). During the experimental trials, body temperature was monitored every minute. Heart rate was measured instantaneously by counting the number of heart beats per minute (from acoustic signals of the recorder), or later analysed from tape recordings, using The Observer event recording program (Noldus Information Technology, The Netherlands).

Heart rate data were converted to their energetic equivalents, according to the equation given by Woakes & Butler (1983) and Bevan & Butler (1992a), as derived from Tufted Ducks swimming at different speeds ($MR = 3.942 \times HR - 3.879$; MR = metabolic rate (W), HR = heart rate (Hz), assuming 20 J per ml oxygen), thereby disregarding individual differences. The energetic costs were expressed as excess costs over resting costs (De Leeuw 1996). Heart rate of resting on water was determined from the lowest heart beat frequency over a period of at least 10 minutes between two series of dives (dive bouts). Excess costs were determined over entire dive bout cycles, i.e. dive bouts and their subsequent recovery periods (Fig. 1). Recovery duration refers to the time of body temperature increase until the pre-dive level was reached. During the experiments the ducks could not rest on land in order to simulate conditions in the wild where Tufted Ducks float on the water surface while resting.

Ducks feeding on mussels

The ducks were housed in an outdoor basin (9.6x4.8 m, 1.5 m deep) at the University of Groningen, The Netherlands. The ducks were fed Zebra Mussels for two months prior to the start of the experiments. Mussels were caught weekly from Lake IJsselmeer at a location frequently used as a feeding site by wild Tufted Ducks. Water temperature in the basin was 4.7–6.2 °C.

Energetic costs of feeding on mussels (handling, shell crushing, and heating up the ingested cold food mass) were determined for mussels with shell lengths between 15 and 20 mm offered at the water surface. These mussels are swallowed singly (De Leeuw & Van Eerden 1992) and food intake could easily be determined by counting the number of mussels ingested. From the frequency distribution on offer and size selection, it was determined that the average mussel ingested weighed 0.8 g fresh weight (gFW), which is equivalent to 0.56 kJ, as determined from the dry

weight of the soft body of mussels and a caloric value of 22.5 kJ.g⁻¹ dry weight).

Food consumption of mussels at a water depth of 1.5 m was determined from the weight loss of clumps of mussels randomly distributed over a net spread over the bottom of the basin. The densities of mussels was low (10–50 gFW.m⁻²) and comparable to late winter feeding conditions in the wild (unpublished data). Food intake rate was estimated from the weight loss of clumps of mussels recollected in the net (after 50–100 dives were observed) and the total dive duration. These experiments were carried out with 2 groups of 3 ducks (two males and one female) per trial to avoid social stress. As diving ducks partly ingest mussels while submerged (De Leeuw & Van Eerden 1992), food intake rates could only be obtained as group averages.

Ducks diving at different depths

After the mussel-feeding experiments, the same ducks were trained for 2 weeks to dive in a 5.7 m deep tank at the Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Vienna (see Carbone *et al.* 1996 and De Leeuw 1996 for details), where they were fed mealworms and mixed grains. Mealworms were preferred and used during experimental trials to stimulate the ducks to dive to a food tray placed at depths between 1.5 and 5.5 m. Five birds, three males and two females, were used in these experiments. The duration of each experimental trial was 2–6 hours and diving depths were 5.5, 1.5, 3.4, 4.4, and 2.5 m, respectively. Water temperature was 10.2 ± 1.3 (7.9–11.5) °C and the difference between surface temperature and temperature at depth never exceeded 0.5 °C.

Two video cameras (one set up at the surface, one at the feeding tray) were used to observe the diving behaviour. The images were mixed down onto a single Panasonic video recorder via a digital AV video mixer and timer (accurate to 0.01 s), while heart rate was recorded via the audio input channel. The behaviour and heart beat frequencies were later analysed from video tapes using The Observer event recording program.

Results

Diving depth experiments

Diving behaviour. Diving was confined to short feed-

Table 1. Mean (SD) durations of different phases of the dive cycle and recovery after a dive bout averaged for 5 Tufted Ducks in relation to diving depth. Water temperature was 10 °C.

Depth (m)	Descent (s)	Foraging (s)	Ascent (s)	Surface (s)	Dive (s)	Dives per bout	Recovery (min)
1.5	2.32 (0.15)	8.09 (2.83)	2.32 (0.19)	11.6 (3.5)	12.7 (3.3)	6.9 (2.9)	24.6 (10.7)
2.5	3.94 (0.37)	9.17 (2.47)	3.29 (0.48)	19.8 (5.2)	16.4 (2.2)	5.8 (2.7)	39.0 (6.0)
3.4	4.77 (0.55)	8.25 (2.03)	4.01 (0.48)	20.6 (5.5)	17.0 (1.6)	3.4 (1.9)	20.9 (11.1)
4.5	6.31 (0.34)	8.75 (1.38)	5.47 (0.93)	19.6 (3.6)	20.5 (0.4)	5.2 (1.9)	47.3 (15.4)
5.5	9.08 (1.26)	12.04 (1.18)	5.34 (0.19)	26.5 (6.4)	26.5 (1.9)	8.4 (4.1)	41.4 (6.3)

ing bouts of a series of 2-14 dives with long resting periods (mean 32 min, S.D. 16 min, maximum 65 min) between dive bouts (example in Fig. 1). After diving the birds were preening or bathing (typically 5-6 min) followed by resting periods with one leg and/or the bill tucked in the feathers to reduce heat loss. Durations of all phases of the dive cycle increased with diving depth (Table 1). Foraging duration, however, exhibited two phases of increase with depth with a dip at about 3-4 m, as has been earlier reported by Carbone *et al.* (1996). Descent speed to the feeding tray was on average 0.66 m.s⁻¹ and did not vary between depths (linear regression, $P > 0.05$). In contrast, ascent speed increased with diving depth from 0.65 m.s⁻¹ at 1.5 m to 1.0 m.s⁻¹ at a diving depth of 5.5 m (linear regression, $r^2 = 0.32$, $P = 0.005$). These values are in good agreement with earlier reported values of Tufted Ducks diving under

equivalent conditions (Carbone *et al.* 1996), suggesting that there was no effect of the transmitters on diving behaviour.

Body temperature. In all trials, body temperature dropped after a number of dives and subsequently it increased gradually (Fig. 1). Highest body temperatures were recorded prior to diving bouts and lowest temperatures during preening and resting immediately after diving (Fig. 2). Post-dive body temperatures decreased with depth (linear regression $r^2 = 0.18$, $P = 0.04$), suggesting that there is no fixed lower threshold temperature which determines the end of a dive bout. The maximum difference in body temperature before and after diving (ΔT_b) increased with the total time spent underwater in a dive bout (Fig. 3; linear regression, $y = 0.0036x + 0.1919$, $r^2 = 0.60$, $P < 0.0001$). Analysis of

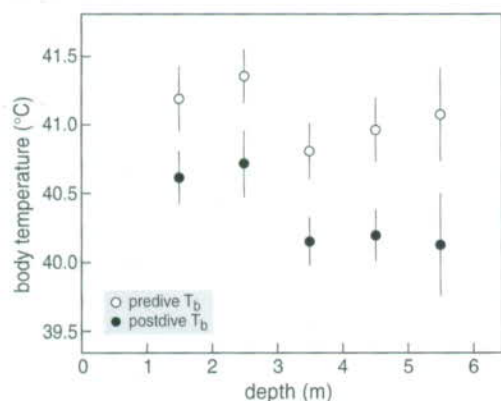
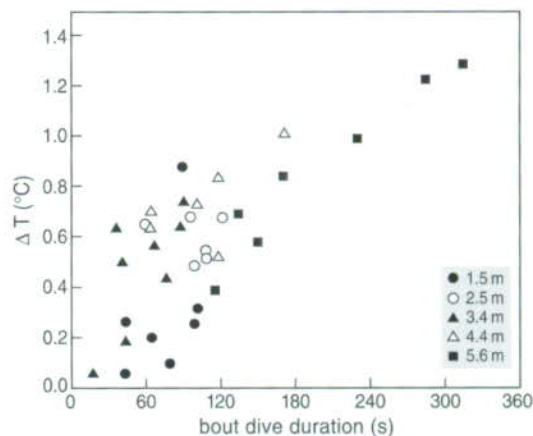
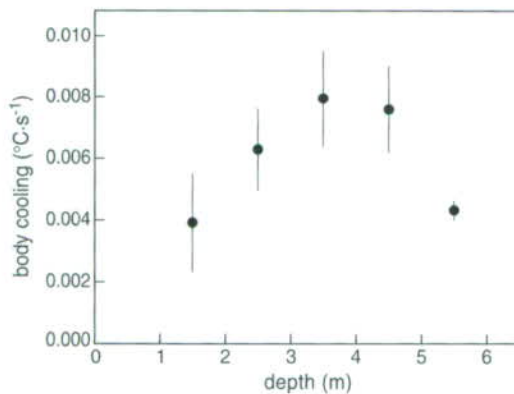
**Fig. 2.** Average maximum and minimum body temperatures (mean and S.D.) before and after diving, respectively, at different feeding depths (water temperature 10 °C).**Fig. 3.** Difference in body temperature before and after diving (ΔT_b) as a function of total dive duration in a feeding bout at different depths.

Table 2. Mean (SD) heart rate (beats.min⁻¹) at rest in water at 10 °C and during different phases of the dive cycle averaged for 5 Tufted Ducks in relation to diving depth.

Depth (m)	Resting	Descent	Foraging	Ascent	Dive	Surface	Bout
1.5	130.0 (9.8)	217.9 (29.4)	209.3 (44.1)	220.6 (40.7)	211.3 (34.5)	241.8 (44.0)	224.5 (34.9)
2.5	129.2 (4.1)	189.7 (29.1)	194.1 (18.2)	211.1 (27.0)	196.5 (18.0)	246.6 (48.1)	222.6 (34.8)
3.4	145.3 (6.4)	211.0 (38.3)	259.2 (73.4)	249.5 (37.1)	245.1 (48.0)	339.5 (44.1)	282.8 (62.1)
4.5	131.2 (8.6)	183.0 (44.2)	192.1 (24.5)	192.2 (27.3)	190.0 (21.3)	264.7 (43.5)	230.5 (44.9)
5.5	133.0 (5.6)	192.5 (25.6)	194.3 (28.2)	214.9 (19.0)	199.2 (21.1)	312.1 (29.5)	253.9 (26.1)
mean	132.7 (8.6)	198.8 (14.9)	209.8 (28.5)	217.7 (20.7)	208.4 (34.8)	312.2 (51.2)	241.1 (44.1)

covariance (ANCOVA) with bout dive duration and diving depth as covariates and individual as factor revealed that ΔT_b varied with depth and the quadratic term of depth (Depth: $F_{1,31} = 11.8$, $P = 0.002$; Depth²: $F_{1,31} = 9.9$, $P = 0.004$). The effect of diving depth on the average cooling rate (°C.s⁻¹ diving) is depicted in Fig. 4, indicating that the cooling rate increased with depth up to 3 or 4 m, but was lower again at the greatest depths. The recovery period was defined as the duration of body temperature increase after cooling by diving. Recovery duration (10 or more min, Table 1) increased with bout dive duration and its quadratic term (stepwise ANCOVA, $P < 0.05$, after backward deletion of depth, the square term of depth and individual differences, $P > 0.05$).

Heart rate and energetics. Resting heart rate of ducks floating on water at 10 °C was on average 130

**Fig. 4.** Body cooling index (°C drop in body temperature per second underwater) in relation to feeding depth.

beats.min⁻¹. Heart rate increased prior to diving and dropped immediately upon submergence. Upon surfacing, and slightly anticipating this, heart rate increased to the highest levels recorded, as illustrated in Fig. 5. Average heart rate was about 200 beats.min⁻¹ during submergence and 290 beats.min⁻¹ between dives of a dive bout (Table 2). Heart rates at different phases of the dive cycle were not related to diving depth (ANOVA, all phases $P > 0.05$). Heart rate between dives tended to increase with depth (ANCOVA with depth as covariate and individual as factor; $P = 0.05$). At a depth of 3.4 m heart rates during resting, diving and surfacing were higher than at other depths (Table 2). It is possible that the higher heart rates observed both during diving and resting in the 3.4 m trials were due to experimental conditions, since heavy

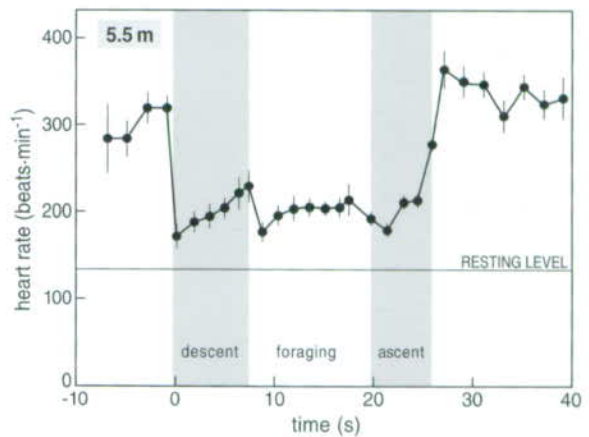
**Fig. 5.** Average heart rate at mean dive duration (± 1 s) of Tufted Ducks diving to 5.5 m ($N = 12$ dives). Shaded areas indicate travel phases of the dive. Resting heart rate was 130 beats.min⁻¹.

Table 3. Correlation matrix of energy, time, and temperature parameters in diving depth experiments of Tufted Ducks. Upper right cells indicate correlation coefficients and *P*-values; lower left cells indicate number of cases. ΔT_b = temperature drop after diving; EEC = excess energy cost.

	Depth	Bout dive duration	Recovery duration	Preening duration	ΔT_b	EEC
Depth	-	0.454 <i>P</i> = 0.001	0.427 <i>P</i> = 0.033	0.026 <i>P</i> = 0.88	0.352 <i>P</i> = 0.26	0.616 <i>P</i> = 0.001
Bout dive duration	48	-	0.561 <i>P</i> = 0.004	0.219 <i>P</i> = 0.17	0.773 <i>P</i> < 0.001	0.686 <i>P</i> < 0.001
Recovery duration	25	25	-	0.240 <i>P</i> = 0.35	0.705 <i>P</i> < 0.001	0.408 <i>P</i> = 0.08
Preening duration	40	40	25	-	0.193 <i>P</i> = 0.26	-0.023 <i>P</i> = 0.91
ΔT_b	40	40	24	36	-	0.649 <i>P</i> = 0.001
EEC	25	25	19	25	25	-

rainfall produced abnormal noise on the roof of the experimental room during these trials. Heart rate was highest between dives or immediately after diving during comfort behaviour like bathing, wing flapping, and preening, and gradually decreased to resting levels (Fig. 1).

The estimated excess energy costs (EEC) increased

with bout dive duration by 42 J per second diving (Fig. 6; linear regression, $r^2 = 0.47$, $P = 0.0002$, $y = 41.7x + 1175$ J; see Table 3 for correlations between activity, cooling, and EEC). Depth had no significant effect on EEC (ANCOVA with dive duration as covariate: $F_{4,19} = 0.85$, $P = 0.51$), but individual differences contributed significantly to the variation ($F_{4,19} = 4.05$, $P = 0.015$).

Mussel-feeding experiments

Diving and feeding behaviour. The thermal conditions at the outdoor basin were more variable than those at the indoor diving tank, due to wind, snow storms, and irradiation in the former. In the surface-feeding trials, the amount of mussels taken per feeding bout (meal size) varied between 1 and 13 gFW (mean 7.0, S.D. 5.0) and meals were separated by short resting intervals of 5.6 min (S.D. 3.9), on average. While diving for mussels at a depth of 1.5 m, meal sizes were larger, varying between 3 and 35 gFW (mean 12.9, S.D. 9.3) and the resting periods between feeding bouts were longer (20.0 min; S.D. 10.5) than in the surface-feeding trials. Mean dive duration was 13.6 s (S.D. 2.4) and the average number of dives in a feeding bout was 8.4 (S.D. 4.0). The average crude food intake rate was calculated over complete feeding bouts including resting episodes between bouts. Crude food intake was 38

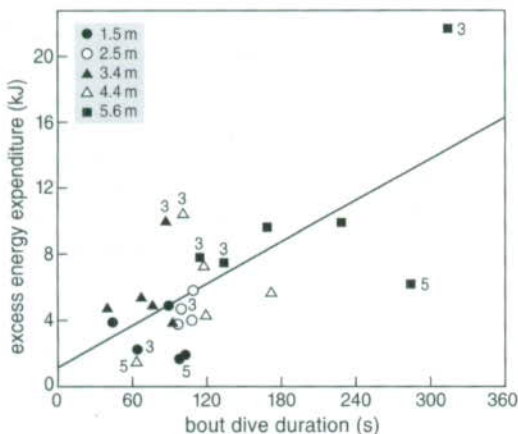


Fig. 6. Increase in excess energy expenditure with bout dive duration at different depths. Labelled data points refer to duck 3 and 5, respectively. The slope of the regression line gives the estimate of excess diving costs of 42 J.s⁻¹.

gFW.h⁻¹ during surface-feeding trials and 27 gFW.h⁻¹ in the diving trials.

Body temperature. Both surface-feeding and diving ducks exhibited a drop in body temperature while ingesting food. In the surface-feeding ducks, body cooling amounted to 0.011 °C.g⁻¹ mussels ($y = -0.011x - 0.034$, $r^2 = 0.34$, $P = 0.0001$). Heat loss in the diving birds was considerably larger and was weakly correlated with meal size of mussels ($r^2 = 0.28$, $P = 0.05$) or bout dive duration ($r^2 = 0.30$, $P = 0.04$), although in a multiple regression analysis both factors were not significant ($P > 0.05$).

Heart rate and energetics. Heart rate during feeding at the surface was on average 154 beats.min⁻¹ (S.D. 8.1), or converted to the energetic equivalent, 6.2 W. While diving for mussels, the average heart rate per feeding bout was 227.7 beats.min⁻¹ (S.D. 20.4), or 11.1 W. Resting heart rates were on average 121.7 beats.min⁻¹ (S.D. 10.1), which amounts to 4.1 W, in both the surface-feeding and diving experiments.

In order to assess the contribution of shell crushing and food heating, the EEC calculated for (surface) mussel-feeding ducks was compared with the theoretical costs of food heating. The warming up costs were estimated from the specific heat of mussels (2.8 kJ.g⁻¹.°C⁻¹) and the mussel consumption (g) and the difference in ambient and body temperature. Surface-feeding costs were only 10% higher than these calculated costs for food heating (Fig. 7) and may partly reflect increased swimming activity while swallowing the mussels. When diving, the costs for feeding on mussels were considerably larger, but not significantly correlated to mussel consumption or bout dive duration ($P > 0.05$).

Discussion

Diving costs

The average metabolic rate estimated from heart rate data during a dive bout (11.4 W) is in good agreement with earlier reported values of ca. 11–14 W obtained by respirometry measurements of diving Tufted Ducks at similar water temperatures (Woakes & Butler 1983, Bevan & Butler 1992a, De Leeuw 1996). The excess

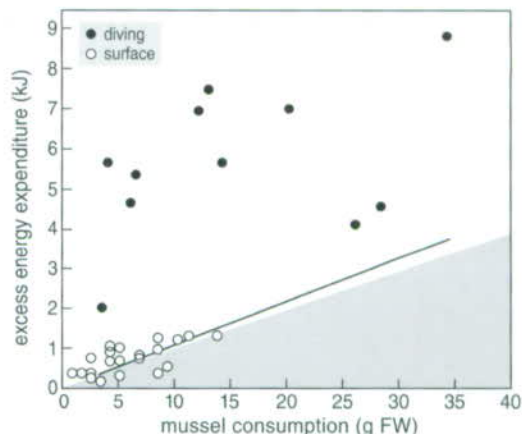


Fig. 7. Excess energy expenditure in relation to mussel consumption of Tufted Ducks feeding at the surface and while diving to 1.5 m. The regression line of the surface-feeding costs is similar to the estimated heat compensation for ingesting the cold mussels (shaded boundary). Excess energy expenditure was higher in the diving birds but not related to mussel consumption.

diving costs estimated from heart rate frequencies during and after diving were on average 42 J.s⁻¹ diving. This value is also very similar to the estimate of 43 J.s⁻¹ for excess diving costs reported by De Leeuw (1996) as obtained from oxygen consumption measurements of Tufted Ducks diving to 2 and 5 m at equivalent water temperatures. In the latter study, excess diving costs increased with lower water temperatures from 23 J.s⁻¹ at 22 °C to 43 J.s⁻¹ at 8 °C, indicating that the thermoregulatory component of diving costs is considerable relative to hydrodynamic costs of diving in cold water. In both studies, the ducks were feeding on mealworms *ad lib*. The ingestion of mealworms of low temperature contributes slightly to the energetic costs. The maximum intake rate of mealworms amounted to 0.04 gFW.s⁻¹ diving. At a water temperature of 10 °C and a body temperature of 41 °C, the compensatory heat production would be 4 J, assuming a specific heat of 3.5 J.g⁻¹.°C⁻¹. By subtraction this would yield a net excess diving cost of 38 J.s⁻¹.

Excess diving costs were not related to diving depth. However, cooling rates increased with depth, but decreased again at the greatest depths. An increase in cooling rate with depth is consistent with the predic-

tion that the increased water pressure at depth reduces the insulation and, therefore, increases heat loss (Kooyman *et al.* 1976, Wilson *et al.* 1992, De Leeuw 1996). It is not clear why this trend did not continue at greater depths. An explanation could be that deeper diving ducks allow more air in the feathers than ducks diving to shallow depths. This would increase the insulation properties of the plumage, while the hydrodynamic cost of overcoming buoyancy remains low at greater depth, because the volume of air is reduced by the increased water pressure at depth. In support of this hypothesis is that descent speed did not vary with depth, despite the expected decrease in buoyancy at greater depths, but ascent speed, which is determined by the upward buoyant force, strongly increased when returning from greater depths (cf. Carbone *et al.* 1996). It is also possible that the peripheral tissues are better perfused while diving to greater depths, to avoid extreme cooling and hypoxic conditions. Carbone *et al.* (1996) hypothesized that Tufted Ducks diving to depths below 4 m have to rely more on anaerobic metabolism than when diving in shallow waters.

Body temperature decreased during diving and feeding bouts and increased between bouts. Thus, the birds were never in thermal balance on the short term. Even when minimal heart rates were recorded between dive bouts, body temperature usually slightly increased. Therefore, the resting metabolic rates obtained in this study probably included some recovery costs from heat loss. As a consequence, the excess costs in this study might be conservative estimates of feeding and diving costs. However, resting metabolic rate estimated from heart rate was 4.7 W in the diving depth experiments and 4.2 W in the mussel-feeding experiments. These values are lower than the 5.7 W reported by Bevan & Butler (1992) and 5.1 W by De Leeuw (1996) which were obtained from respirometry data at equivalent temperatures. A reason for the discrepancy could be that the average oxygen pulse of a heart beat is larger in thermoregulating resting animals than in active animals. This phenomenon has been observed in Oystercatchers *Haematopus ostralegus* resting and walking, respectively, at different ambient temperatures (O. Hüppop and M. Kersten, pers. comm.) and deserves further study. For Tufted Ducks resting at low water temperatures, oxygen consumption was slightly higher (ca. 10%) than predicted from the heart

rate of actively swimming ducks (Fig. 4 in Bevan & Butler 1992a). Although the absolute estimate of metabolic rates may be biased, the effect on excess costs may be small. Our estimates of excess diving costs from heart rate data (which include also the long periods of resting while body temperature gradually increased) were very similar to respirometry measurements under equivalent conditions. Therefore, we tentatively conclude that possible differences in oxygen pulse did not affect the estimates of excess energy costs in our study.

Feeding costs

When the ducks were feeding on mussels offered at the surface, the excess energy cost (EEC) was very similar to the estimated obligatory cost of thermoregulation to compensate the heat loss from ingesting cold mussels (Fig. 7). This suggests that the costs of shell crushing are extremely low or that the heat generated by the gizzard muscles while crushing the shells was substituting for the thermoregulatory heat production imposed by ingesting cold food. Nehls (1995) demonstrated that crushing costs in Eiders feeding on *Mytilus* shells amount to 75% of the resting metabolic rate in winter and that the costs increase exponentially with shell size. He also showed that ca. 50% of the heat generated for shell crushing could substitute thermoregulatory costs at low ambient temperatures when thermostatic costs were 40% higher than at thermoneutrality. At higher thermoregulatory demands (e.g., more than 100% in excess of basal costs in the present study), a larger proportion or all heat may be substituted (see below). Taking into account that in the surface-feeding trials the ducks consumed large mussels (16–20 mm), i.e. in the upper range of their normal diet (De Leeuw & Van Eerden 1992), we conclude that shell crushing does not contribute to the daily energy budget as an excess over thermoregulatory costs under the severe thermal conditions prevailing during winter.

Similarly, the heat production from digestion can substitute for thermoregulation, as has been demonstrated in mollusc-feeding Eiders (Nehls 1995) and Sea Otters *Enhydra lutris* (Costa & Kooyman 1984) and Muskrats feeding on aquatic vegetation (MacArthur & Campbell 1994). In the latter studies, the digestive heat was used for thermoregulation while the animals were resting in water at low temperatures. From a consider-

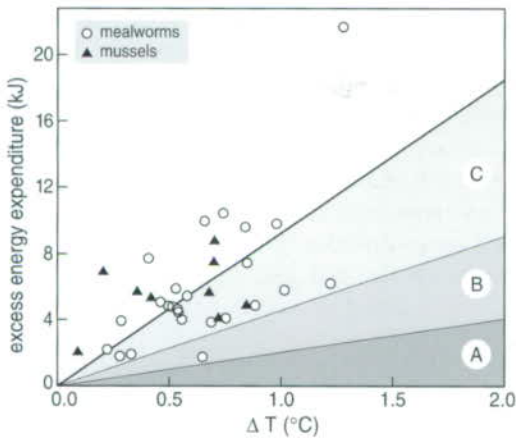


Fig. 8. Relationship between excess energy expenditure and the difference in body temperature before and after diving (ΔT_b). There was no difference in slope between feeding on mussels and feeding on mealworms. The estimated thermoregulatory component of diving is composed of the post-dive costs of heating up the body after the temperature drop (A) and the ongoing thermoregulatory heat production during diving (B), while the remaining fraction refers to estimated hydrodynamic costs of diving (C).

ation of energetic balance they would otherwise have needed to generate heat by increasing their activity. Wilson & Culik (1991) also demonstrated in Adélie Penguins *Pygoscelis adeliae* that the elevation in metabolic rate after a meal of cold krill could be fully explained by the need to warm up the ingested meal in the stomach without assuming additional digestive costs. This confirms Kleiber's (1961) suggestion that all digestive heat could be substituted if the thermoregulatory demands exceed the digestive heat production.

In conclusion, only the thermoregulatory component of food processing costs contributes to the daily energy budget of Tufted Ducks feeding on mussels in winter. De Leeuw *et al.* (in prep.) estimated that feeding costs amount to 15% of the energy budget, as estimated from the compensatory heat production for food ingestion.

Functional relationship between cooling and energy costs

In periods of high thermoregulatory demand, probably all heat generated by food processing in the core tissues can be used for thermoregulation (Kleiber 1961). It is

questionable whether this also holds for heat generated by diving activity. Heat generated during terrestrial locomotion can be partly or, at extreme low temperatures, fully substitute for thermoregulatory costs (e.g., Pohl & West 1973, Paladino & King 1984, Zerba & Walsberg 1992). During diving, however, the movement of the hind limbs for locomotion might increase conductive and convective heat loss and the heat generated in the limbs may be difficult to conserve, because blood flow distribution in the peripheral tissues is greatly reduced (Bevan & Butler 1992b). Indeed, excess diving costs heavily depend on water temperature (De Leeuw 1996), indicating that heat generation by activity is insufficient to compensate heat loss at low water temperatures.

The functional relationship between the extent of body cooling and energy costs of diving is further explored in Fig. 8. In our experiments, a temperature drop of 1 °C in the abdomen was accompanied by an increase in EEC of 9.1 kJ in all experiments. The contribution of the recovery from a drop in body temperature to EEC can be estimated from the energy cost to increase body temperature of a 600 g Tufted Duck, assuming a specific heat of 3.45 J.g⁻¹ (Hart 1951). This would amount to 2.1 kJ.°C⁻¹, under the simplified assumption that the observed body cooling in the abdominal cavity would be representative for the entire body. Warming up the body would then explain 23% of the excess costs (Fig. 8). This fraction is paid during the preening and resting phase after a dive bout. The remaining costs comprise the hydrodynamic costs of overcoming buoyancy and drag (Lovvorn & Jones 1991) and the elevated thermoregulatory costs during the dive bout (until the end of the drop in body temperature). From the relationship between EEC and water temperature mentioned above (De Leeuw 1996), it can be estimated that the thermoregulatory component attributes at least 50% to the diving costs under cold conditions. Since 23% is expended after diving, approximately 27% of the diving costs would be devoted to extra thermoregulation during a dive bout to prevent the body from further cooling. Indeed, it has been demonstrated that in colder water the overall diving metabolic rate is higher in Tufted Ducks (Bevan & Butler 1992a, De Leeuw 1996), but insufficient to maintain a constant body temperature.

Impact of body cooling on time and energy budgets

Crude food intake rate was 38 gFW.h⁻¹ when ducks were feeding on mussels at the surface and 27 gFW.h⁻¹ when diving. To meet the daily energy demands of *ca.* 1800 gFW mussels per day (De Leeuw *et al.*, in prep.), the crude food intake rate of Tufted Ducks must be at least 75 gFW.h⁻¹. Assuming that intake rate was maximal during feeding bouts, recovery durations between meals should be reduced more than twofold to meet their daily food requirements. In the diving trials, the average drop in abdominal temperature after a meal of *ca.* 13 gFW amounted to 0.49 °C, followed by a recovery period of 20 minutes on average, while under semi-natural conditions the resting periods between dive bouts are less than 10 minutes (unpublished data). This raises the question whether shorter recovery durations incur higher energy costs. The relationship between recovery time and metabolic heat production was simulated using a Newtonian model of body cooling with compensation by heat production:

$$T_b - T_a = (T_i - T_a) \exp(-tK/C) + (MR/K)(1 - \exp(-tK/C)),$$

where T_b is body temperature (°C) at time t (s), T_a is ambient water temperature (°C), T_i is the initial body temperature (°C), K is the dry thermal conductance (W.°C⁻¹), C is the heat capacitance of the animal (J.°C⁻¹), assuming a specific heat of 3.45 J.g⁻¹, and MR is the metabolic rate (W). K and MR were corrected for evaporative heat loss (EHL, 0.7 W, as obtained from the evaporative water loss of 1 g.h⁻¹ of Tufted Ducks at ambient temperatures below 15 °C (De Leeuw *et al.*, in prep.) and the latent heat of vaporization of water of 2.427 kJ.g⁻¹ (Schmidt-Nielsen 1975)). The thermal conductance was estimated from the metabolic rate of Tufted Ducks resting on water (De Leeuw 1996), according to the equation $K = (MR - EHL) / (T_b - T_a)$.

This model was used to calculate the (recovery) time for an increase by 0.5 °C in body temperature from an initial temperature of 40.5 °C in relation to the metabolic heat production at ambient water temperatures of 5 and 10 °C, respectively (Fig. 9). Figure 9 illustrates that a slight increase in metabolic rate (just above the metabolic rate at thermal balance) can

greatly reduce recovery times, but metabolic rate must be considerably higher to recover from a 0.5 °C drop in body temperature within 10 minutes.

Although the model assumes that the total excess cost for increasing body temperature is independent of the metabolic rate (and thus recovery duration), there may be important differences in thermal conductance related to metabolic heat production. During the longer recovery periods, metabolic rate is close to the resting level, and thermal conductance is minimal while floating quietly on the water surface with the bill and one leg tucked in the feathers. Skin temperatures of Eiders floating on cold water were about 30 °C, while the core body temperature was 40.4 °C, suggesting that peripheral vasoconstriction was used to reduce thermal conductance (Jenssen *et al.* 1989). However, when resting durations between dive bouts have to be as short as 10 min to meet the daily energy demands, metabolic rate must be increased by 15%, according to the model (Fig. 9). This can probably be realized only by shivering thermogenesis or heat generated by activities like preening (Croll & MacLaren 1993, De Leeuw 1996), grooming (MacArthur 1984) or swimming (Costa & Kooyman 1984). Activity, however, might also in-

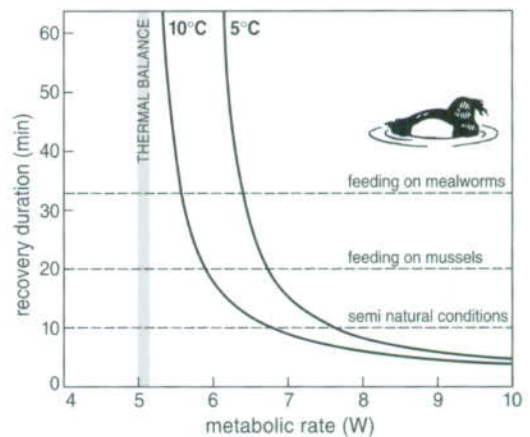


Fig. 9. Recovery duration as a function of metabolic rate for a 600 g Tufted Duck increasing its body temperature of 40.5 °C by 0.5 °C at a water temperature of 5 °C and 10 °C, according to Newtonian cooling with compensation by metabolic heat production (see text). The metabolic rate at thermal balance is 5 W at 10 °C and 5.8 W at 5 °C (De Leeuw 1996). Observed recovery durations in our experiments and under semi-natural conditions (unpublished data) are indicated by the broken lines.

crease conductance and is, therefore, less efficient than long resting periods. Wilson & Culik (1991) also argue that endotherms living in cold environments should spread their feeding activity by long resting periods between meals in order to optimise the use of digestive and activity-generated heat for thermoregulation.

In diving ducks wintering on cold water with energy budgets close to their metabolic ceiling (Nehls 1995, De Leeuw *et al.*, in prep.), we may expect a tendency for long resting durations between meals. During extreme cold spells, diving ducks, that are normally night-active, extend their feeding activity during the day (e.g., Michot *et al.* 1993, Nilsson 1972), which may reflect a shift to longer resting periods between meals at night in addition to increased food requirements. On the other hand, it may be disadvantageous to spend too much time resting between feeding bouts at the feeding grounds, where the birds may be exposed to strong winds and wave action, which might increase heat loss. Most species of diving ducks do, indeed, prefer to rest during the day-time hours at sheltered areas (Suter 1982, Pedroli 1982, Burger 1983). From an energetic perspective, resting periods thus seem of great importance in order to balance the energy budget.

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References

Bevan, R.M. & Butler, P.J. 1992a. The effects of temperature on the oxygen consumption, heart rate and deep body temperature

during diving in the Tufted Duck *Aythya fuligula*. *J. Exp. Biol.* 163: 139-151.

Bevan, R.M. & Butler, P.J. 1992b. Cardiac output and blood flow distribution during swimming and voluntary diving of the Tufted Duck *Aythya fuligula*. *J. Exp. Biol.* 168: 199-217.

Bevan, R.M., Speakman, J.R. & Butler, P.J. 1995. Daily energy expenditure of Tufted Ducks: a comparison between indirect calorimetry, doubly labelled water and heart rate. *Funct. Ecol.* 9: 40-47.

Blaxter, K. 1989. Energy metabolism in animals and man, Cambridge University Press, Cambridge.

Burger, J. 1983. Factors affecting distribution of Greater Scaup *Aythya marila* in a coastal estuary in New York, USA. *Ornis Scand.* 14: 309-316.

Carbone, C., de Leeuw, J.J. & Houston, A.I. 1996. Adjustments in the diving time budgets of Tufted Duck and Pochard: is there evidence for a mix of metabolic path ways? *Anim. Behav.* 51: 1257-1268.

Costa, D.P. & Kooyman, G.L. 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the Sea Otter *Enhydra lutris*. *Physiol. Zool.* 57: 199-203.

Croll, D.A. & McLaren, E. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. *J. Comp. Physiol. A* 163: 160-166.

De Leeuw, J.J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in Tufted Ducks. *Can. J. Zool.* 74: 2131-2142.

De Leeuw, J.J. & Van Eerden, M.R. 1992. Size selection in diving Tufted Ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. *Ardea* 80: 353-362.

De Leeuw, J.J., Van Eerden, M.R. & Visser, G.H. (in prep.) Wintering Tufted Ducks *Aythya fuligula* diving for Zebra Mussels *Dreissena polymorpha* balance feeding costs within narrow margins of their daily energy budget.

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. *Physiol. Zool.* 68: 1143-1163.

Hart, J.S. 1951. Calorimetric determination of average body temperature of small mammals and its variation with environmental conditions. *Can. J. Zool.* 29: 224-233.

Jenssen, B.M. & Ekker, M. 1989. Thermoregulatory adaptations to cold in winter-acclimatized Long-tailed Ducks *Clangula hyemalis*. In C. Bech & R.E. Reinertsen (Eds.): *Physiology of cold adaptations in birds*, Plenum Press, New York, pp. 147-152.

Jenssen, B.M., Ekker, M. & Bech, C. 1989. Thermoregulation in winter-acclimatized Common Eiders *Somateria mollissima* in air and water. *Can. J. Zool.* 67: 669-673.

- Kleiber, M. 1961. The fire of life. Wiley, New York.
- Kooyman, G.L., Gentry, R.L., Bergman, W.P. & Hammel, H.T. 1976. Heat loss in penguins during immersion and compression. *Comp. Biochem. Physiol. A* 54: 75-80.
- Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W. & Sinnett, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell Seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol. A* 138: 335-346.
- Lovvorn, J.R. & Jones, D.R. 1991. Effects of body size, body fat, and changes in pressure with depth on buoyancy and costs of diving in ducks *Aythya* spp. *Can. J. Zool.* 69: 2879-2887.
- MacArthur, R.A. 1984. Aquatic thermoregulation in the Muskrat *Ondatra zibethicus*: energy demands of swimming and diving. *Can. J. Zool.* 62: 241-248.
- MacArthur, R.A. & Campbell, K.L. 1994. Heat increment of feeding and its thermoregulatory benefit in the Muskrat *Ondatra zibethicus*. *J. Comp. Physiol. A* 164: 141-146.
- McNab, B.K. 1980. On estimating thermal conductance in endotherms. *Physiol. Zool.* 53: 145-156.
- Michot, T.C., Moser, A.B. & Norling, W. 1993. Effects of weather and tides on feeding and flock positions of wintering Redheads in the Chandeleur Sound, Louisiana. *Hydrobiol.* 1-16.
- Nehls, G. 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente *Somateria mollissima*. D.Ph.Thesis. Christian-Albrechts Universität, Kiel.
- Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. *Ornis Scand.* 3: 55-78.
- Paladino, F.V. & King, J.R. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion in White-crowned Sparrows *Zonotrichia leucophrys*. *Physiol. Zool.* 57: 226-236.
- Pedroli, J.-C. 1982. Activity and time budget of Tufted Ducks on Swiss lakes during winter. *Wildfowl* 33: 105-112.
- Pohl, H. & West, G.C. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the Common Redpoll. *Comp. Biochem. Physiol. A* 45: 851-867.
- Prinzinger, R., Pressmar, A. & Schleucher, E. 1991. Body temperature in birds. *Comp. Biochem. Physiol. A* 99: 499-506.
- Schmidt-Nielsen, K. 1975. *Animal Physiology*. Cambridge University Press, Cambridge.
- Stahel, C.D. & Nicol, S.C. 1982. Temperature regulation in the Little Penguin *Eudyptula minor* in air and water. *J. Comp. Physiol. A* 148: 93-100.
- Stephenson, R. 1994. Diving energetics in Lesser Scaup *Aythya affinis* Eyton. *J. Exp. Biol.* 190: 155-178.
- Stephenson, R., Butler, P.J. & Woakes, A.J. 1986. Diving behaviour and heart rate in Tufted Ducks *Aythya fuligula*. *J. Exp. Biol.* 126: 341-359.
- Suter, W. 1982. Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala*, *Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/Hochrhein (Bodensee). *Orn. Beob.* 79: 225-254.
- Webster, M.D. & Weathers, W.W. 1990. Heat produced as a by-product of foraging activity contributes to thermoregulation by Verdins *Auriparus flaviceps*. *Physiol. Zool.* 63: 777-794.
- Wiersma, P., Piersma, T. & Van Eerden, M.R. 1995. Food intake of Great Crested Grebes *Podiceps cristatus* wintering in cold water as a function of various cost factors. *Ardea* 83: 339-350.
- Wieser, W. 1989. Energy allocation by addition and by compensation: an old principle revisited. In W. Wieser & E. Graiger (Eds.): *Energy transformations in cells and organisms*. Thieme, New York, pp. 98-105.
- Wilson, R.P. & Culik, B.M. 1991. The cost of a hot meal: facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. *Comp. Biochem. Physiol. A* 100: 151-154.
- Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E. & Nöldeke, C.E. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Am. Nat.* 140: 179-200.
- Woakes, A.J. & Butler, P.J. 1983. Swimming and diving in Tufted Ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. *J. Exp. Biol.* 107: 311-329.
- Zerba, E. & Walsberg, G.E. 1992. Exercise generated heat contributes to thermoregulation by Gambel's Quail in the cold. *J. Exp. Biol.* 171: 409-422.

Chapter 7

Wintering Tufted Ducks *Aythya fuligula* diving for Zebra Mussels *Dreissena polymorpha* balance feeding costs within narrow margins of their energy budget

Joep J. de Leeuw, Mennobart R. van Eerden & G. Henk Visser

Submitted



Wintering Tufted Ducks *Aythya fuligula* diving for Zebra Mussels *Dreissena polymorpha* balance feeding costs within narrow margins of their energy budget

Diving ducks face the strongly cooling properties of the aquatic environment. In experiments with Tufted Ducks *Aythya fuligula* feeding on Zebra Mussels *Dreissena polymorpha* in outdoor cages, we measured changes in food consumption and diving behaviour in relation to water temperature. Water efflux and daily energy expenditure (DEE) were measured using doubly labelled water. Tufted Ducks swallow whole mussels and crush shells in the gizzard. Due to the low flesh content of mussels, daily mussel consumption was extremely high (up to 3 times the body mass of 600 g in winter). Water efflux was 6.5 to 13 times higher than allometrically predicted (Nagy & Peterson 1988), with a maximum of 1.1 L.d⁻¹. As a consequence of high water turnover rates, DEE estimates from doubly labelled water measurements were variable, but were on average in good agreement with DEE estimates obtained from food consumption and time-energy budgets (ca. 5% higher values). DEE increased with lower temperatures from ca. 2.5 (summer) to more than 4 times the basal metabolic rate (winter). Costs for thermoregulation and heating up the ingested mussels primarily explained the high DEE in winter. At lower temperatures, dive duration was shorter and less time was spent selecting small sized mussels at the bottom, while more larger mussels were brought up and were ingested at the water surface. Thereby, the energetic costs for crushing shells probably increased in favour of a reduction in diving costs. The narrow margins of the energy budget, wherein feeding costs must be balanced, imply that food availability and water temperature may determine the regulation of population numbers of diving ducks.

Introduction

Due to the high thermal conductivity of water, an aquatic life style seems energetically expensive for diving birds wintering in areas with low water temperatures (De Vries & Van Eerden 1995). The energetic costs to maintain a constant body temperature when resting in water are considerably higher than when resting on land for diving ducks (Jenssen & Ekker 1989, Jenssen *et al.* 1989), guillemots (Croll & McLaren 1993), and penguins (Kooyman *et al.* 1976, Stahel & Nicol 1982). Diving for food in cold water increases heat loss, since the body is surrounded by water (De Vries & Van Eerden 1995, De Leeuw 1996) and hydrostatic pressure reduces the thickness of the insulating air-layer trapped in the feathers (Kooyman *et al.* 1976, Wilson *et al.* 1992). Feeding birds also undergo internal cooling when ingesting food with a con-

siderably lower temperature than their body temperature. Heating up the ingested food mass may also result in a considerable elevation of the energy expenses (e.g. Wilson & Culik 1991).

A variety of studies suggests that the daily energy budget of aquatic birds is related to water and air temperature, although, to our knowledge, energy expenditure has never been measured in a direct fashion. Daily foraging times, for example, have been reported to increase with lower temperatures in wintering diving ducks (Nilsson 1972, Goudie & Ankney 1986, Nehls 1995), suggesting that more food is required to balance a higher heat loss during colder periods. Food intake of Great Crested Grebes *Podiceps cristatus*, as reconstructed from stomach contents, increased almost twofold from summer to winter (Wiersma *et al.* 1995). Nehls (1995) estimated from field observations that the daily intake of Blue Mussels *Mytilus edulis* by Eiders

Somateria mollissima increased by almost 50% from summer to winter. Studies on body mass changes suggest that diving ducks are in a negative energetic balance during the coldest months when they rely on their fat reserves (Ryan 1972, Lovvorn 1994, Suter & Van Eerden 1992). These considerations suggest that the metabolic scope of diving birds in winter may be limited, owing to high feeding costs at low water temperatures, and, consequently, food availability and energetic costs may be important factors regulating population numbers (Von Haartman 1971).

We measured DEE and examined the energetic implications of living in cold water in the Tufted Duck. In western Europe, Tufted Ducks mainly winter on large freshwater lakes with temperatures close to freezing, where they feed on Zebra Mussels *Dreissena polymorpha*. Mussels are caught during dives of up to 5 m deep. Whole mussels are swallowed and subsequently crushed in the gizzard. In experiments with captive Tufted Ducks diving under semi-natural conditions, we measured daily food consumption and diving activity of ducks feeding on Zebra Mussels at water temperatures between 22 °C (late summer) and less than 3 °C (winter). Water flux and DEE were also determined using the doubly-labelled water technique (validated in Tufted Ducks by Bevan *et al.* (1995)), demonstrating that these small-sized aquatic birds live close to an assumed 'metabolic ceiling' owing to high thermostatic costs in winter.

Methods

Ducks feeding on mussels in diving cages

Tufted Ducks were successfully trained to dive for Zebra Mussels in individual diving cages under semi-natural conditions. Due to a limited capacity of collecting a continuously large supply of fresh mussels during six months and the limited number of diving cages available for mussel-feeding ducks, only three individuals (2 males, 1 female) could be used in the experiments. Each cage had a surface area of 1x1 m and it was 5 m deep (Fig. 1). The cages consisted of open wire-mesh shafts fixed to a pontoon that was located in an 8 m deep sand pit (10 ha) frequently visited by wild Tufted Ducks. The ducks were exposed to all weather conditions, but wave action was buffered by 0.5 m high panels at the surface (to 0.3 m under the water surface).

Water temperature was measured daily at 10 cm beneath the surface. Monthly measurements at depths up to 5 m showed that the water column was well-mixed with deviations of less than 1.5 °C between bottom and surface temperatures. Fresh mussels were offered daily on a food tray that could be moved through the dive shaft to manipulate diving depth. Fresh Zebra Mussels

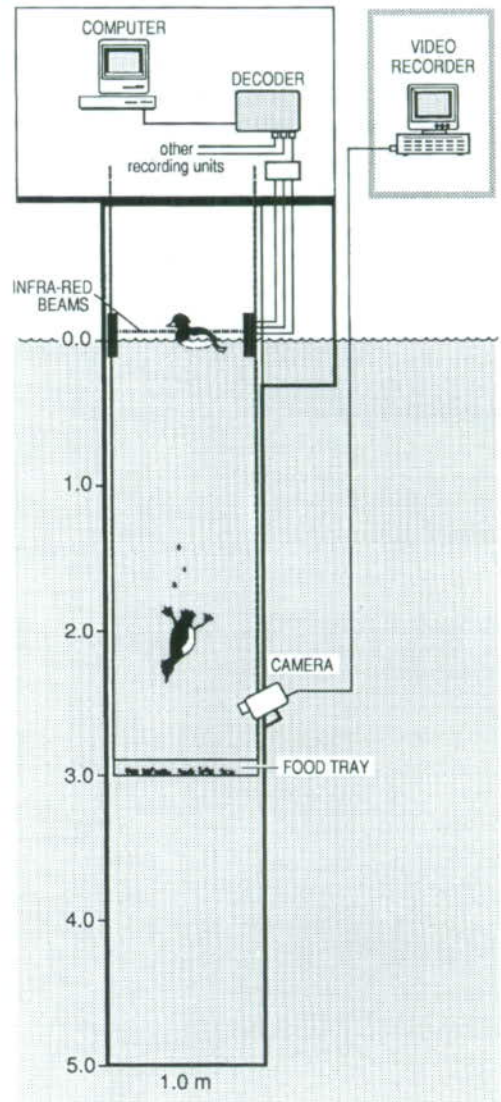


Fig. 1. Illustration of one diving cage. The food tray could be moved by ropes to manipulate diving depth. Diving activity was recorded using a computer-controlled system with infra-red light beams.

were caught weekly in the adjoining Lake IJsselmeer, The Netherlands, from a favourable feeding location used by wild ducks. The birds were fed on Zebra Mussels for four months prior to all measurements in order to adjust the digestive tract to this food (see Piersma *et al.* 1993).

Diving activity was recorded day and night using a purpose-built infrared-light system. Recording units in each cage consisted of 12 parallel infrared-light beams (CY-R2MD sensors and reflectors mounted on a floating frame of 0.95x0.95m) covering the entire surface area. A Husky Hunter data logger was used to calculate dive durations accurate to 1 s of each of the birds simultaneously. An underwater camera (OSPREY OE 1306; 6mm, f1.4, angle 63°) was used to check the system and to obtain additional information on the feeding behaviour at the food tray.

Each day around noon the ducks were caught, weighed, and placed in small, dark boxes. The food trays were lifted to the surface and the remaining mussels were collected and weighed. A new batch of mussels (of known fresh weight) was supplied and the food tray was moved to depth again (1 m, 3 m, or 5 m). The amount of food offered was dependent on consumption rate, such that no more than 60 % of the available food would be consumed to avoid depletion of the food source. After 1-2 h, the ducks were released again in their cages. Food consumption was measured as the weight difference of mussels before and after an experimental period of *ca.* 22 h.

Calculations of DEE

Daily mussel consumption was converted to metabolizable energy intake (MEI) using a conversion factor of 0.6 kJ.g⁻¹ fresh mass of mussels. This value was obtained from observed size selection, flesh content of differently sized mussels, the energetic equivalent of 22.5 kJ.g⁻¹ dry flesh mass (no seasonal trends, A. bij de Vaate, pers. comm.), and water content of mussels, and assuming an assimilation efficiency of 85% as determined in mussel-eating Oystercatchers *Haematopus ostralegus* (M. Kersten, pers. comm.). Size selection was measured from samples of 300-600 g drawn before and after feeding (details in De Leeuw & Van Eerden 1992) during doubly labelled water trials (see below). Selectivity for size classes was determined from the selectivity index $D = (r-p)/(r+p-2rp)$, where r

and p are the fraction of a size class in the diet and on offer, respectively (Jacobs 1974). The nutritional value of differently sized mussels (dry weight of the soft body, DW) was determined from the same samples (10 individuals per even mm size class of mussels with shell lengths (L) between 8 and 22 mm): $DW(mg) = 0.0074 \times L^{2.742}$ ($r^2 = 0.97$).

DEE and water flux were estimated using a mixture of D₂O and H₂¹⁸O for H₂O turnover and CO₂ production at water temperatures between 3 °C and 23 °C and diving depths of 1 m, 3 m, and 5 m (2, 9, and 6 data points, respectively). DEE of Tufted Ducks estimated by the doubly labelled water technique has previously been validated under laboratory conditions with birds feeding on corn (Bevan *et al.* 1995). Different calculation models were tested. Equation [4] in Speakman (1993), a model assuming different body water pools for the hydrogen and oxygen isotopes and correcting for fractionation effects in evaporated water, proved to be most appropriate in these birds. However, we used the two-pool calculation model of Heymans & Roberts (1990), which is basically similar to the equation of Speakman (1993), but is more flexible with respect to the incorporation of estimates of evaporative water loss (EWL) (see Appendix for a detailed description of the method and equations). For comparison, DEE was also calculated according to Speakman (1993).

The doubly labelled water method is based on the difference in clearance rates of ²H and ¹⁸O isotopes from the body water pool (Lifson & McClintock 1966). Prior to administration of isotopes, the natural abundances of ²H and ¹⁸O were determined by filling 4 to 8 microcapillaries with 15 µl blood, after puncturing the *vena recurrens ulnaris* with a needle. The capillaries were flame sealed. Next, 1 ml of isotope mixture of about 60 atom percent ¹⁸O, and 30 atom percent ²H (enrichments of the different mixtures exactly known) was injected in the abdominal cavity using a calibrated syringe. In some cases, however, it was noted that a droplet was spilled during injection. To determine the proper equilibration time (highest enrichment of isotopes), 1 male weighing 550 g was injected with 0.5 ml isotope mixture. The bird was subsequently placed in a small box without food, and blood samples were taken at 1, 2, 3, and 4 hours after injection time. It appeared that 1.5 h was the optimal time interval between injection and taking the initial sample, which was used in all

experimental birds. After having taken this sample, the ducks were released in their diving cages. After 22.5 to 23.8 h the ducks were caught again and final blood samples were taken immediately. All blood samples were stored at 5 °C and analyzed in triplicate by the Centre for Isotope Research in Groningen, The Netherlands (for details see Masman & Klaassen 1987, and Nolet *et al.* 1992).

Evaporative water loss (EWL) was measured in 4 adult ducks (average body mass 531 g) using the open flow method as described by Lasiewski *et al.* (1966). During the measurement, the bird was situated on a grid above a 1-cm layer of paraffin oil to prevent evaporation of water from faeces. Air temperature in the respiration chamber was 10 °C, i.e. below the lower critical temperature of *ca.* 18 °C of the ducks in air in winter (De Leeuw, unpublished data), to estimate minimal EWL (Dawson 1982). Incurrent air (150 L.h⁻¹; measured with a mass-flow controller, Brooks 5850 E)

passed through a glass tube containing water absorbing predried molecular sieve granules (3 Å). After acclimatization for 1 h the excurrent air was dried over a molecular sieve and the mass increase of the sieve was measured at intervals of 1 h until 60% of the water retaining capacity of the sieve (after 4.2 to 5.9 h) was reached.

Results

Food intake

Daily mussel consumption of Tufted Ducks varied between less than 1 kg fresh mass in summer (after moult) and an average of 1.5–2 kg (i.e., 3 times body mass) in winter. Body mass varied between 510 and 695 g with mean masses of 582, 609, and 607 g for the female [F1] and the males [M1, M2], respectively. No seasonal trends were detected (linear regression, $P > 0.05$ in all individuals), but daily fluctuations in body mass measurements were considerable, because a single defaecation (mainly shell fragments and water) could cause a mass loss of up to 25 g. The mass-specific metabolisable energy intake (MEI, kJ.kg⁻¹.d⁻¹) increased with lower water temperatures ($r^2 = 0.50$, $P < 0.0001$; Fig. 2), and was not significantly different between depths (ANCOVA with temperature as covariate; $F_{2,74} = 1.17$, $P = 0.32$), nor between individuals ($F_{2,74} = 0.89$, $P = 0.42$).

DEE estimates from doubly labelled water measurements varied considerably (coefficient of variation 33%, Table 1), as earlier reported by Bevan *et al.* (1995) for the Tufted Duck. DEE estimated according to Speakman (1993) was on average 4.6 % lower than when estimated according to Heymans & Roberts (1990). Given the 12.5 % underestimation of DEE according to Speakman's equation in the validation study in Bevan *et al.* (1995), we conclude that our estimates of energy expenditure might be slightly conservative. Mass-specific DEE (according to Heymans & Roberts 1990) compared well with the MEI calculated from food intake (average deviation *ca.* 6%, see Fig. 2), although the trend with water temperature was not significant ($r^2 = 0.23$, $P = 0.07$).

DEE estimated from the daily mussel consumption reached an extremely high level of *ca.* 1800 kJ.kg⁻¹.d⁻¹ or 1080 kJ.d⁻¹ for a 600-g bird at low water tempera-

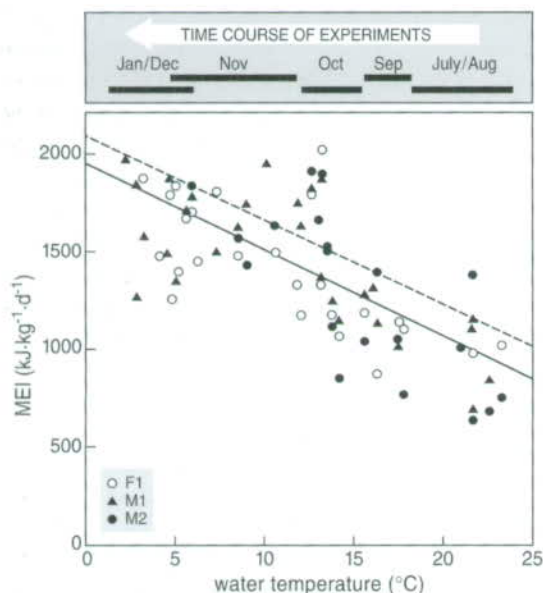


Fig. 2. Daily metabolisable energy intake (MEI, calculated from consumption of Zebra Mussels) in relation to water temperature in three Tufted Ducks feeding in diving cages (data points and solid line, $y = 2287 - 51.6x$, $r^2 = 0.50$, $P < 0.0001$). DEE estimated from doubly labelled water measurements is plotted for comparison (dashed line, $y = 2073 - 41.7x$, $N = 16$, $r^2 = 0.23$, $P = 0.07$). The upper pannel indicates temperature ranges per month.

Table 1. Daily mussel consumption, water flux and energy expenditure of individual Tufted Ducks during doubly labelled water experiments. T_w is water temperature ($^{\circ}\text{C}$), BM is body mass (g), C is mussel consumption (g fresh mass), W_i en W_e are water fluxes calculated from water intake via mussels and from isotopic water turnover, respectively, DEE is daily energy expenditure calculated from Heymans & Roberts (1990), DEE_{S93} from equation [4] in Speakman (1993).

Date	T_w ($^{\circ}\text{C}$)	Depth (m)	Duck	BM (g)	C (gFW)	W_i (g.d $^{-1}$)	W_e (g.d $^{-1}$)	DEE (kJ.d $^{-1}$)	DEE_{S93} (kJ.d $^{-1}$)
11 Jul	21.6	5	F1	525	870	537	649	800	766
	21.6	5	M2	553	650	401	626	888	850
	21.6	5	M3	525	560	346	613	671	644
13 Jul	20.8	5	M2	555	1280	791	981	656	625
	20.8	5	M3	535	1430	883	932	1125	1070
13 Sep	17.8	3	F1	600	1100	679	703	678	651
	17.8	3	M2	590			610	513	495
	17.8	3	M3	633	770	476	686	374	363
4 Oct	16.1	1	M2	570	1270	784	833	941	897
	16.1	1	M3	615	1435	886	838	1001	954
2 Nov	12.1	3	F1	640	1255	775	813	497	477
	12.1	3	M2	593	1630	1007	1000	1427	1354
	12.1	3	M3	608	1840	1136	1094	1175	1115
28 Nov	5.1	5	M2	618	1380	852	1005	1041	989
5 Dec	2.9	3	M2	623	1890	1167	1001	1235	1173
3 Jan	3.6	3	F1	578	1230	760	854	1144	1089

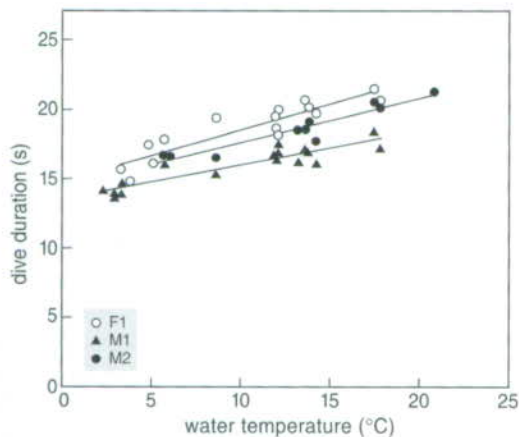


Fig. 3. Dive duration in relation to water temperature for the three Tufted Ducks diving at a feeding depth of 3 m (F1: $y = 14.8 + 0.37x$, $r^2 = 0.82$, $P < 0.0001$; M1: $y = 13.5 + 0.27x$, $r^2 = 0.85$, $P < 0.0001$; M2: $y = 14.1 + 0.34x$, $r^2 = 0.90$, $P < 0.0001$).

tures (3°C) during winter. This is approximately 4.2 times the basal metabolic rate (BMR) of 257 kJ.d^{-1} measured in 6 Tufted Ducks (Daan *et al.* 1990) and approximated the average maximum of 1200 kJ.d^{-1} , as predicted by Kirkwood (1983) for a bird of this size in his review on maximum metabolisable energy intake. This energetic level is also close to the metabolic scope of 5 BMR predicted for birds under cold stress (Hinds *et al.* 1993).

Diving and feeding behaviour

The average duration of a dive decreased in colder water, being *ca.* 25 % shorter in winter as compared to summer conditions at a feeding depth of 3 m (Fig. 3; individual differences were significant: $F_{2,36} = 42.6$, $P < 0.001$, ANCOVA with water temperature as covariate, $P < 0.001$). In contrast to these mussel feeding ducks, dive duration of Tufted Ducks feeding on mealworms at equivalent depth was 20 s and did not vary with water temperature over the same range (Carbone *et al.* 1996).

The number of feeding dives to a depth of 3 m was about 200 in summer, but increased to more than 350

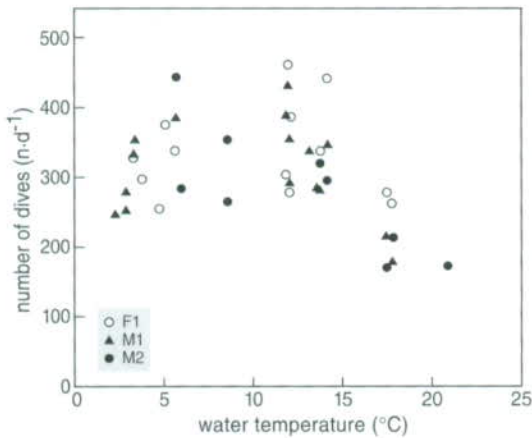


Fig. 4. Number of dives per day in relation to water temperature for the three Tufted Ducks diving at a feeding depth of 3 m ($y = 198 + 30.5x - 1.5x^2$, $r^2 = 0.39$, $P = 0.0001$).

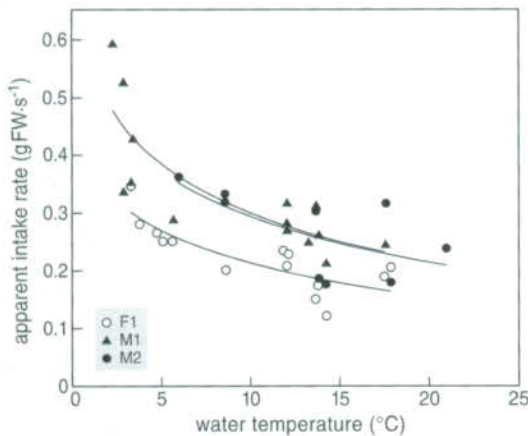


Fig. 5. Apparent food intake rate as a function of water temperature for the three Tufted Ducks diving at a feeding depth of 3 m (F1: $\log y = 0.145 - 0.552 \log x$, $r^2 = 0.78$, $P < 0.0001$; M1: $\log y = 0.309 - 0.498 \log x$, $r^2 = 0.87$, $P < 0.0001$; M2: $\log y = 0.376 - 0.619 \log x$, $r^2 = 0.54$, $P < 0.05$).

in autumn followed by a slight decrease in winter when temperatures were below 10 °C (Fig. 4). A significant quadratic function with water temperature (T_w) could be fit through the data (linear regression, $r^2 = 0.39$, $P = 0.0001$; T_w : $t = 3.9$, $P = 0.002$; T_w^2 : $t = 3.4$, $P = 0.004$).

The apparent food intake rate was calculated as the daily mussel consumption divided by daily time spent diving (rather than actual feeding time, as the birds also

swallow mussels at the water surface). Because daily food intake increased with lower temperatures (Fig. 2) and dive duration and the number of dives per day decreased at the lowest temperatures, the apparent food intake rate increased at water temperatures below 10 °C (Fig. 5). The apparent intake rate in the slightly smaller female was lower than in the males (ANCOVA on \log_{10} - \log_{10} transformed data, $F_{2,33} = 28.1$, $P < 0.001$, with the logarithm of water temperature as covariate, $P < 0.001$). The increase in apparent intake rate in cold water was probably due to a shift in foraging method. Observations of feeding birds demonstrated that Tufted Ducks can swallow mussels underwater, but also take mussels to the water surface, in particular large-sized mussels or clumps of mussels kept together by byssal threads. At high temperatures, the ducks spend probably more time per dive (reflected by longer dive durations) at the feeding tray to select small-sized mussels (shell length less than 16 mm) that can easily be swallowed under water in contrast to larger mussels (De Leeuw & Van Eerden 1992). When feeding in cold water larger mussels or clumps are probably more frequently brought up to the surface. Indirect evidence supports this hypothesis: selectivity for the preferred smaller size classes (< 16 mm) slightly decreased with lower water temperatures ($t = 3.6$, $P = 0.002$; average D was 0.2 in summer and 0.1 in winter), suggesting indeed that the ducks refrained from searching for small mussels in cold water.

Effect of water depth on diving performance

The diving performance at different water depths is compared for winter conditions with water temperatures below 10 °C (Table 2). Food intake did not vary between diving depths (Student's t -test, $P > 0.05$), although it is uncertain whether the ducks were in energy balance at a diving depth of 5 m, as appeared from the average daily body mass change of -5 g. Due to the large variation in body mass measurements (as a consequence of large effects of a single defaecation), this value did not deviate significantly from the other depths.

The number of dives at a feeding depth of 1 m was more than 50% higher than at 3 m and 5 m. Dive duration increased with diving depth (Table 2). Thus, the daily time spent diving was highest at the greatest depth (1.35 h, 1.38 h, and 1.68 h, at diving depths of 1,

Table 2. Food intake and feeding behaviour (mean and standard deviations) of three Tufted Ducks diving at different feeding depths during winter conditions with water temperatures below 10 °C.

	Depth (m)		
	1	3	5
n	11	21	8
Food intake (gFW.d ⁻¹)	1661 (242)	1572 (296)	1623 (193)
Dive duration (s)	9.8 (1.9) **	15.8 (1.6) **	20.9 (1.9)
Number of dives per day	497 (37) **	315 (47)	290 (40)
Apparent intake rate (gFW.s ⁻¹)	0.35 (0.08)	0.32 (0.11) *	0.27 (0.05)
Body mass (g)	601 (29)	586 (38)	580 (54)
Body mass change (g.d ⁻¹)	-1.3 (10.4)	-1.1 (13.0)	-5.5 (5.3)

Significant differences between depths are indicated by asterisks (Student's *t*-test, * $P < 0.05$, ** $P < 0.001$).

3, and 5m, respectively) and the apparent intake rate was significantly lower at 5m.

Water flux in relation to feeding behaviour

Water efflux varied between 610 and 1094 ml.d⁻¹ (mean 827 ml.d⁻¹, Table 1). Hughes *et al.* (1987) predicted from literature data a water flux of 124.8 ml.d⁻¹ for a 600 g bird with salt glands. In their review of water flux rates, Nagy & Peterson (1988) compiled allometric relationships which predict a water flux rate of 85-87 ml.d⁻¹ for 600 g non-passerine birds or for seabirds of that size. Deviations from allometric predictions never exceeded 3 times the predicted value. However, flux rate in ducks feeding on mussels in our study was 6.5 (summer) to 13 times (winter) the predicted value (Fig. 6). For comparison, we plotted water flux rate measured in 4 ducks fed on pellets in an aviary with a 2x2 m basin (0.5 m deep) using D₂O. Water flux was on average 172 ml.d⁻¹ at an air temperature of 10 °C, thus twice the predicted value. Bevan *et al.* (1995) also found a relatively high water flux of 239 ml.d⁻¹ in diving Tufted Ducks feeding on corn (Fig. 6). In aquatic birds, the imminent contact with surrounding water may increase water turnover. The extra water exchange probably occurs across respiratory surfaces with saturated air and also via the skin, for example across the large surface area of the webs (Bevan *et al.* 1995), but the high water flux in ducks feeding on mussels is obviously a consequence of 'bulk-feeding', i.e. ingesting whole mussels including shell and water.

If the water balance of the ducks is in equilibrium, intake of water from mussels (60% of mussel mass)

plus metabolically produced water calculated from catabolizing fat, protein and carbohydrates (Schmidt-Nielsen 1975) of mussel flesh should equal water efflux measured with ²H (assuming complete mixture of isotopes with body water). Water efflux calculated from ²H turnover was higher than this predicted value, when the ducks were feeding at greater depth (ANCOVA, all depths $F_{2,11} = 4.04$, $P < 0.05$, excluding the limited data at 1 m and comparing only the 3m and 5m data, $F_{1,10} = 5.80$, $P < 0.05$, see Fig. 7). The slope of the regression lines of 3 and 5 m was significantly greater

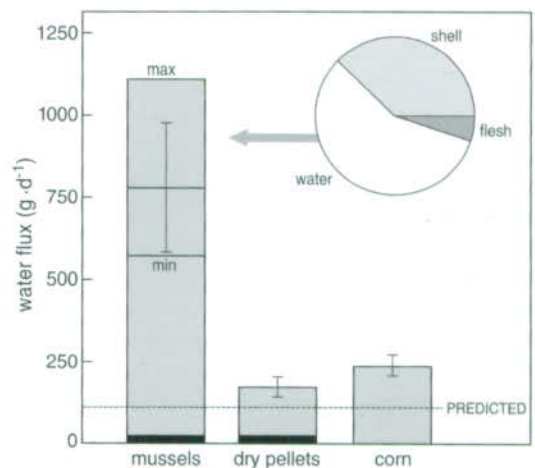


Fig. 6. Water flux (mean \pm S.D., minimum and maximum) in Tufted Ducks feeding on Zebra Mussels, dry food pellets, and corn (from Bevan *et al.* 1995), respectively. The fraction of water evaporated is indicated black. Pie-chart gives the composition of Zebra Mussels.

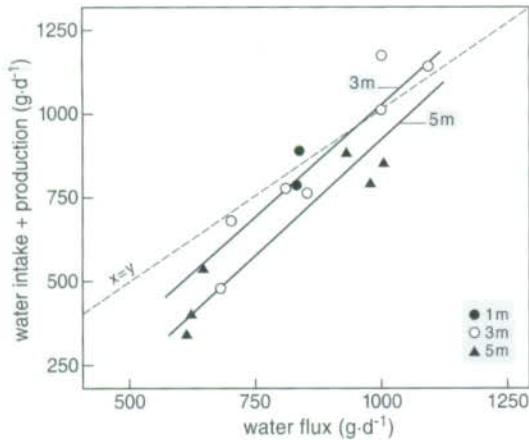


Fig. 7. Water intake from mussels and metabolically produced water against water flux. The regression lines of 3 m and 5 m differ significantly from $y = x$ ($P < 0.05$), with a common slope (1.35) and different intercepts (-328 and -445, respectively).

than one ($t_{12} = 2.5$, $P < 0.05$), with the largest deviation at the lower flux rates. This suggests that at low flux rates, the ducks ingested more water than that entrapped in the mussel shells. This is presumably a consequence of the feeding habits of the ducks. As mentioned earlier, Tufted Ducks tend to lift more mussels to the surface before swallowing under cold conditions, while at higher temperatures most mussels are swallowed at the food tray. Swallowing mussels at the bottom may incur the ingestion of additional water collected in the bill together with the mussels. Also, in deep dives (5m), the ducks feed longer at the bottom (Carbone *et al.* 1996), thereby ingesting more mussels with extra water, before they take mussels to the surface, than in shallower dives (3m). The extra water mass ingested by deeper diving ducks enhances the internal cooling. Thus, foraging costs increase as prey at greater depth is exploited due to both increased external cooling (reduced insulation) and internal cooling (extra water ingested), although we could not detect an effect of diving depth on DEE.

Discussion

DEE in relation to water temperature

DEE increased by 70% from summer (2.5 BMR) to

winter (4.2 BMR). These values are higher than reported by Bevan *et al.* (1995) for Tufted Ducks diving under laboratory conditions (1.7 BMR at a water temperature of 18 °C to 2.8 BMR at 7 °C). The higher DEE's in our study are probably due to the high costs of feeding on mussels with a low energy density (Figures 2 and 6), while diving activity was comparable in both studies (1.3-1.4 h·d⁻¹). In addition, the outdoor weather conditions (wind and waves, see below), to which our ducks were exposed, could contribute to a higher DEE. A similarly high DEE and strong relationship between DEE and temperature was found in Eiders feeding on Blue Mussels in the German Wadden Sea. From field observations of food intake, Nehls (1995) calculated an increase in DEE from 3 to 4.3 BMR from summer to winter. Wiersma *et al.* (1995) approximated DEE of Great Crested Grebes at Lake IJsselmeer from stomach content analysis, yielding an increase from *ca.* 3 to 5 BMR from autumn to winter.

The contribution of different energetic components to the daily energy budget in summer and winter can be estimated from diving activity and food consumption data and the different cost factors reported in the literature (Table 3). The components are expressed as costs in excess over maintenance costs (basal and thermoregulatory costs at rest).

Maintenance costs were estimated from the equation given by De Leeuw (1996) from oxygen consumption measurements of Tufted Ducks resting on the water surface at temperatures between 8 and 22 °C. The additional cost of compensating the cooling effect of the cold food mass passing through the body was calculated from the caloric value to heat up the food from ambient water temperatures to a body core temperature of 41 °C (Bevan & Butler 1992), assuming a specific heat of 4.2 J·g⁻¹·°C⁻¹ for water (60% of ingested mass) and 0.8 J·g⁻¹·°C⁻¹ for the calcareous shell (*ca.* 40% of food mass, the 2 to 5% dry flesh was neglected). The food heating component contributed 7 to 18% to the daily energy costs in summer and winter, respectively. Thus, the energy spent to maintain a constant body temperature (thermoregulation and heating food) was *ca.* 60% of the DEE. It must be noted that actual thermostatic costs may be even higher, due to extra conductive heat loss from wind (Wiersma & Piersma 1994), wave action in the cages, and movement of the birds.

Table 3. Estimated energy budget of Tufted Ducks (body mass 600 g) diving for Zebra Mussels in winter (water temperature 3 °C) and summer (20 °C). Components are expressed as kJ.d⁻¹ in excess over maintenance (basal plus thermoregulatory) costs. DEE was estimated from food intake.

Component	Winter	Summer	Reference
Maintenance	508	318	De Leeuw 1996
Food heating	194	45	This study
Diving	232	107	De Leeuw 1996
Shell crushing	38	62	Nehls 1995
Digestion (HIF)	102	122	Nehls 1995
Total	1074	654	
DEE	1080	640	This study

The contribution of diving costs to the energy budget was estimated from the diving activity (1.4 hours per day both in summer and winter) and the diving costs in excess over resting costs in Tufted Ducks diving at different temperatures (26 and 50 J per second diving in summer and winter, respectively; De Leeuw 1996). Part of the diving costs thus reflects a further increase in thermoregulatory costs. Diving costs added 17% (summer) to 21% (winter) to the daily energy budget.

The contribution of energy costs for food processing to DEE (crushing the shells in the gizzard by muscle power and digestion of food) is not straightforward, as the heat production can substitute for thermoregulatory costs (Wieser 1989). In captive Eiders (1.8 kg) feeding on Blue Mussels, Nehls (1995) found that 8–28% (increasing exponentially with shell sizes in the range of 30 to 60 mm) of the assimilated energy at thermoneutrality was used for crushing mussel shells in the gizzard and 19% of the assimilated energy for digestion (heat increment of feeding, HIF). At low ambient temperatures (–20 °C in air, equivalent to 5 °C at sea), however, the additive costs for shell crushing and digestion were 60 and 50% lower, respectively, due to heat substitution. Similarly, in Sea Otters *Enhydra lutris*, 60% of thermoregulatory costs were covered by HIF shortly after a meal of clams *Spisula solldissima* (Costa & Kooyman 1984). Tufted Ducks feed on considerable smaller shells (10–20 mm) than Eiders, while the relative increase in thermoregulatory costs from

summer to winter is higher (40% of BMR in Eiders, 70% in Tufted Duck, De Leeuw 1996). Therefore, the additive crushing costs are probably lower in Tufted Duck than in Eider and may not contribute significantly to DEE in winter (as suggested by heart rate measurements of Tufted Ducks feeding on *Dreissena*, unpublished data). We approximated the contribution of costs for processing the mussels in our study by assuming similar relative costs for digestion as in Nehl's study on mussel-feeding Eiders (19 and 9.5% of assimilated energy in summer and winter, resp.), and 50% lower relative costs than those in Eiders for crushing the much smaller sized *Dreissena* mussels (9 and 4% of assimilated energy in summer and winter, resp.).

The sums of the estimated components of the energy budgets in summer and winter are in very good agreement with our estimates of DEE from food consumption, deviating only by ca. 2% (Table 3). As mentioned earlier, maintenance costs may be underestimated for ducks exposed to wind and waves, while the digestive heat may be overestimated, because a greater proportion could substitute if thermoregulatory demand increases (Dawson & O'Connor 1996).

Behavioural implications

DEE in winter seems to be close to the maximum energy expenditure as predicted by Kirkwood (1983) and Hinds *et al.* (1993). To a large degree this is due to the high costs for thermoregulation. Therefore, in winter the energetic window for activity and food processing seems to be restricted and strong cooling conditions may have a great impact on the behaviour of the ducks.

The increase in apparent food intake rate with lower water temperatures (Fig. 5) seems to be based on balancing diving costs and food processing costs (crushing shells and digestion). For example, under summer conditions the ducks were probably able to reduce their diving costs by 40% by bringing up mussels to the surface as they did in winter, thereby reducing the total energy expenditure in summer by 6%. However, selecting small-sized mussels is probably more profitable under these conditions as the thinner shells and higher flesh content incur lower food processing costs than when feeding on larger mussels (De Leeuw & Van Eerden 1992, Nehls 1995). In contrast, the costs for selecting small sized mussels in cold water increase, owing to a higher heat loss while diving. In addition, the

relative costs for crushing large shells are lower under cold conditions, if heat production from this activity can largely substitute the increased thermoregulatory costs. Selection for small sizes would therefore become less profitable in winter.

'Chilling' factors like wind, low air temperatures, wave action, etc., increase the convective heat loss and may drive the energetic costs of diving ducks to their maximum. During times of high thermoregulatory demand (strong winds and low air temperatures), Red-heads *Aythya americana* and Tufted Ducks increase their diurnal feeding activity (in addition to their normally nocturnal diving activity; Michot *et al.* 1993, Nilsson 1972). Diving ducks usually roost in large flocks sheltered from wind. Suitable roosting areas are often at considerable distance from feeding areas. For example, Goldeneyes *Bucephala clangula* fly up to 40 km between roosting and feeding areas (Saylor & Afton 1981), and Tufted Ducks 5-15 km (Nilsson 1972, own observations), indicating that diving ducks may balance high flight costs (Masman & Klaassen 1987) by savings on thermoregulatory costs.

In our study, heat production to compensate heat loss from food ingestion was calculated at 15% of the DEE in winter. Flesh content of mussels was only ca. 5% of the ingested mass. In Lake IJsselmeer, mussels from deeper water tend to have lower flesh contents (at 5 m ca 40% lower than at 2 m, unpublished data). The total food mass that has to be processed to meet daily energy needs should therefore increase with diving depth. This might limit the exploitation of deeper located mussel beds in addition to greater diving efforts in deeper water (Table 2).

In conclusion, wintering diving ducks have to balance high feeding costs and low energetic returns from mussels within narrow margins of the energy budget, imposed by the strongly cooling aquatic environment. Several studies indicate a negative energy balance for diving ducks in the coldest months (Ryan 1972, Kestenholtz 1994, Lovvorn 1994). Indeed, poor foraging conditions and long cold spells, may cause mass starvation in diving ducks (Suter & Van Eerden 1992), and population numbers may be regulated by winter mortality (Von Haartman 1971).

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References

- Berger, M., Hart, J.S. & Roy, O.Z. 1971. Respiratory water and heat loss of the Black Duck during flight at different ambient temperatures. *Can. J. Zool.* 49: 767-774.
- Bevan, R.M. & Butler, P.J. 1992. The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the Tufted Duck *Aythya fuligula*. *J. Exp. Biol.* 163: 139-151.
- Bevan, R.M., Speakman, J.R. & Butler, P.J. 1995. Daily energy expenditure of Tufted Ducks: a comparison between indirect calorimetry, doubly labelled water and heart rate. *Functional Ecol.* 9: 40-47.
- Carbone, C., De Leeuw, J.J. & Houston, A.I. 1996. Adjustments in the diving time budgets of Tufted Duck and Pochard: is there evidence for a mix of metabolic path ways? *Anim. Behav.* 51: 1257-1268.
- Costa, D.P. & Kooyman, G.L. 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the Sea Otter *Enhydra lutris*. *Physiol. Zool.* 57: 199-203.
- Crawford, E.C. & Lasiewski, R.C. 1968. Oxygen consumption and respiratory evaporation of the Emu and Rhea. *Condor* 70: 333-339.
- Croll, D.A. & McLaren, E. 1993. Diving metabolism and thermoregulation in Common and Thick-billed Murres. *J. Comp. Physiol. A* 163: 160-166.
- Daan, S., Masman, D. & Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* 259: R333-R340.
- Dawson, W.R. 1982. Evaporative losses of water by birds. *Comp. Biochem. Physiol. A* 71: 495-509.
- Dawson, W.R. & O'Connor, T.P. 1996. Energetic features of avian thermoregulatory responses. In: C. Carey (Ed.) *Avian Ener-*