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Brünnich's guillemots (*Uria lomvia*) maintain high temperature in the body core during dives

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Abstract

A major challenge for diving birds, reptiles, and mammals is regulating body temperature while conserving oxygen through a reduction in metabolic processes. To gain insight into how these needs are met, we measured dive depth and body temperatures at the core or periphery between the skin and abdominal muscles simultaneously in freely diving Brünnich's guillemots (*Uria lomvia*), an arctic seabird, using an implantable data logger (16-mm diameter, 50-mm length, 14-g mass, Little Leonardo Ltd., Tokyo). Guillemots exhibited increased body core temperatures, but decreased peripheral temperatures, during diving. Heat conservation within the body core appeared to result from the combined effect of peripheral vasoconstriction and a high wing beat frequency that generates heat. Conversely, the observed tissue hypothermia in the periphery should reduce metabolic processes as well as heat loss to the water. These physiological effects are likely one of the key physiological adaptations that makes guillemots to perform as an efficient predator in arctic waters.
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1. Introduction

Diving seabirds encounter an energetic conflict between maintaining high body temperatures to maximize power output from muscle and the need to extend aerobic dive time in cold water. First, for most endothermic animals, a high and constant body temperature is thought to have important influence on power generation by muscles in cold water, e.g. in the pursuit of prey (Alexander, 1999). Raising the temperature increases the rate of enzyme-catalyzed reactions. Faster reactions enable muscles to exert more power. However, the thermal conductivity of salt water is 25 times greater than that of air, and the specific heat of water is four times grater, resulting in much

Table 1
Diving profile of individual birds, showing number of dive cycles, mean dive depth, mean duration of dives and mean duration of resting periods

Year	ID no.	Number of dive cycles	Mean dive depth (m)	Mean duration of dives (s)	Mean duration of resting periods (s)
Birds recording T_{bc}					
2000	#00	283	12.1±5.6	69.9±15.8	46.3±23.2
2001	#L3	571	22.4±24.6	65.5±44.5	48.7±51.3
2001	#U2	405	33.7±21.1	107.5±31.6	70.8±42.2
Birds recording T_{bp}					
2001	#U30	716	18.9±12.8	75.1±25.1	38.5±26.1

The sampling year and identification (ID) number of birds are also indicated. Means are given with standard deviation.

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Table 2
Diving profile of individual birds, showing number of dive bouts, mean duration of dive bouts, and mean dive depth and mean number of dives within a dive bout

Year	ID no.	Number of dive bouts	Mean duration of dive bouts (min)	Mean dive depth (m) within a dive bout	Mean number of dives within a dive bout
Birds recording T_{bc}					
2000	#00	14	40.3±21.9	12.4±4.4	21.4±4.4
2001	#L3	31	36.6±24.1	41.9±25.0	22.9±40.6
2001	#U2	29	43.7±19.3	37.8±17.7	15.0±6.5
Birds recording T_{bp}					
2001	#U30	35	40.2±19.5	20.4±13.9	21.5±11.7

The sampling year and identification (ID) number of birds are also indicated. Means are given with standard deviation.

higher heat loss in water (Kaseloo and Lovvorn, 2005). Secondly, glycolysis produces less ATP per mole of glucose than the Krebs cycle, and that it takes longer at the surface to remove lactate from the blood before diving again than after aerobic dives. Therefore, it is generally thought that diving seabirds use aerobic metabolism in most serial dives (Butler and

Jones, 1997; Kooyman and Ponganis, 1998; Ponganis and Kooyman, 2000; Schmidt et al., 2006). Past research has shown that the body temperature of birds can drop during dives in cold water, which probably lowers metabolic rate (outside of exercising muscles) and thereby allows extension of aerobic dive duration (Culik et al., 1996; Bevan et al., 1997; Handrich et al., 1997; Butler, 2000).

Most superior diving seabirds, such as penguins and alcids, are limited in distribution to areas of cold water (Stonehouse, 1967; Ainley and Boekelheide, 1983). Therefore, it is unclear how small endothermic animals like seabirds regulate their body temperature when diving in water that is so much colder than their body temperatures.

Brünnich's guillemots (*Uria lomvia*) are diving seabirds that belong to the family Alcidae. They are important predators in northern marine ecosystems (Gaston and Jones, 1998). They use their wings both to fly and to dive to depths more than 100 m in search of highly mobile prey (Guderley, 1990; Croll et al., 1992; Gaston and Jones, 1998; Watanuki et al., 2001), and this should result in a compromise in their locomotor physiology (Lovvorn and Jones, 1994). Nevertheless, considering their small body size (usually <1 kg), they dive longer than do
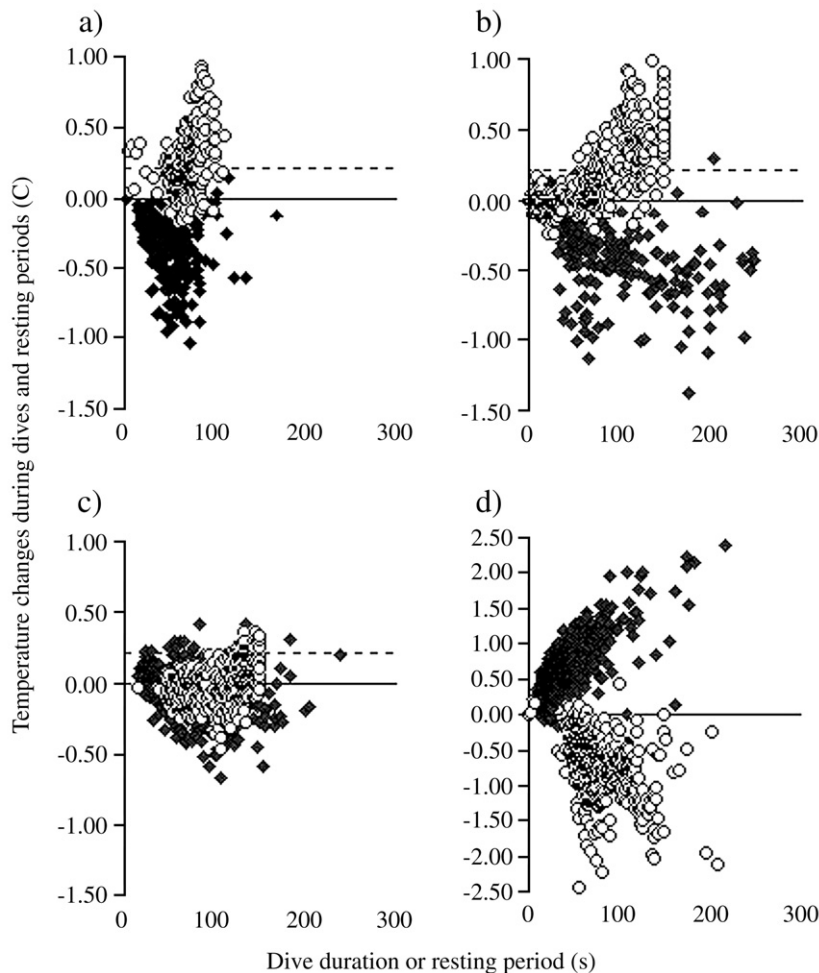

Fig. 1. Relationship between dive duration or resting period, and changes in body temperature. (a), (b), (c) and (d) were showed birds #00, #L3, #U2 and #U30. Open circles and closed lozenges showed body temperature changes during diving and resting periods, respectively. The dotted line indicated temperature of 0.21 °C.
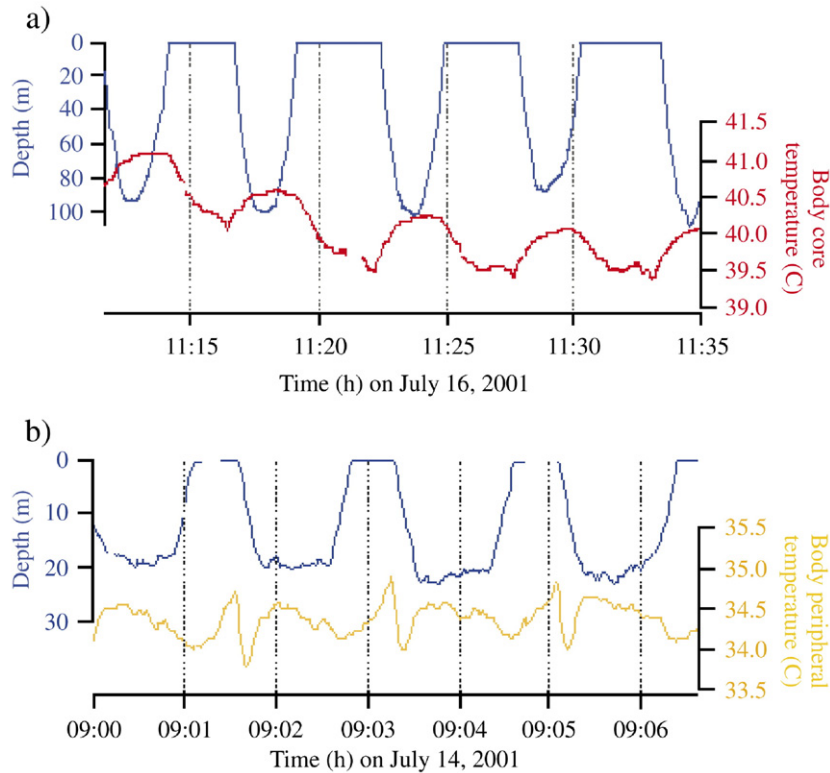
Fig. 2. An expanded view of the temperature changes in (a) body core (T_{bc}) and (b) body periphery (T_{bp}) corresponding to diving activity during individual non-foraging dives. (a) and (b) graphs are T_{bc} and T_{bp}, respectively. The upper and lower lines of the graph represent the diving profiles and body temperatures, respectively. T_{bc} increases while diving but decreases during subsequent periods of resting at the sea surface. In contrast to T_{bc}, T_{bp} decreases during dives but increases during the following resting time.

penguins (Watanuki and Burger, 1999). Furthermore, with a smaller body mass and relatively larger surface area compared to penguins, guillemots may experience greater reductions in body temperature to spare oxygen while diving in cold water. To elucidate the energetic challenges of diving in a small seabird species, we measured the temperature changes at the body core (T_{bc}) and body periphery (T_{bp}) in freely diving Brünnich's guillemots using implanted data-loggers.

2. Materials and methods

Guillemots brooding chicks in a colony at Kongsfjorden, Svalbard (78°54′N, 12°13′E) were caught at the nest site in the summer of 2000 and 2001 (Watanuki et al., 2001, 2003). Under general anesthesia (isoflurane gas and mixed with oxygen), M190-DT loggers (16-mm diameter, 50-mm length, 14-g mass, Little Leonardo Ltd., Tokyo) enveloped with biocompatible silicon were implanted in the body cavities of four birds. These devices recorded temperature and depth at 1 s intervals. Temperature sensors (accuracy of ±0.1 °C) were placed under the right liver lobe near the heart, lung, and pectoral muscles in three birds. This region is defined as the body core. In another guillemot, a sensor was inserted between the skin of the abdomen and the abdominal muscles: a region we considered to be the body periphery. Guillemots were released near the colony within 3 h of capture after they were provided enough resting

time to recover from the surgery. All four birds returned to the nest to brood within a day. After 4–8 days post surgery, the birds were recaptured and devices surgically removed. They also returned to the nest within two days after devices were removed. The present study was approved by the Norwegian Animal Research Authority and the Governor of Svalbard.

A total of 1377 dives were recorded from the three birds whose T_{bc}s were measured and 742 dives were recorded from the other bird where T_{bp} was measured. Dive depth and temperature data were analyzed using custom-written software (LOG TOOLs, Marine Micro Technology) and Igor Pro (Wave Metrics). The dive depth, dive duration, surface interval, body temperature change from the start to the end of dives and during subsequent resting periods were determined for each dive cycle. A dive was defined as the maximum depth deeper than 0.5 m. Guillemots made serial dives that were divided by a bout-ending criterion (Gentry and Kooyman, 1986). We determined the bout-ending criterion based on Sibly et al. (1990). For the analysis, we considered only those dive bouts that had at least 4 dives and the last dive in a bout was excluded from the analysis.

To compare body temperatures of two phase behaviours (diving and brooding), birds' behaviours on their nests were observed. Bird #00 brooded on their nests during the period between 2:10 and 4:45, 11, July 2000, and birds #L3, U2 and U30 during the periods between 20:45 and 21:15, 15, July 2001.
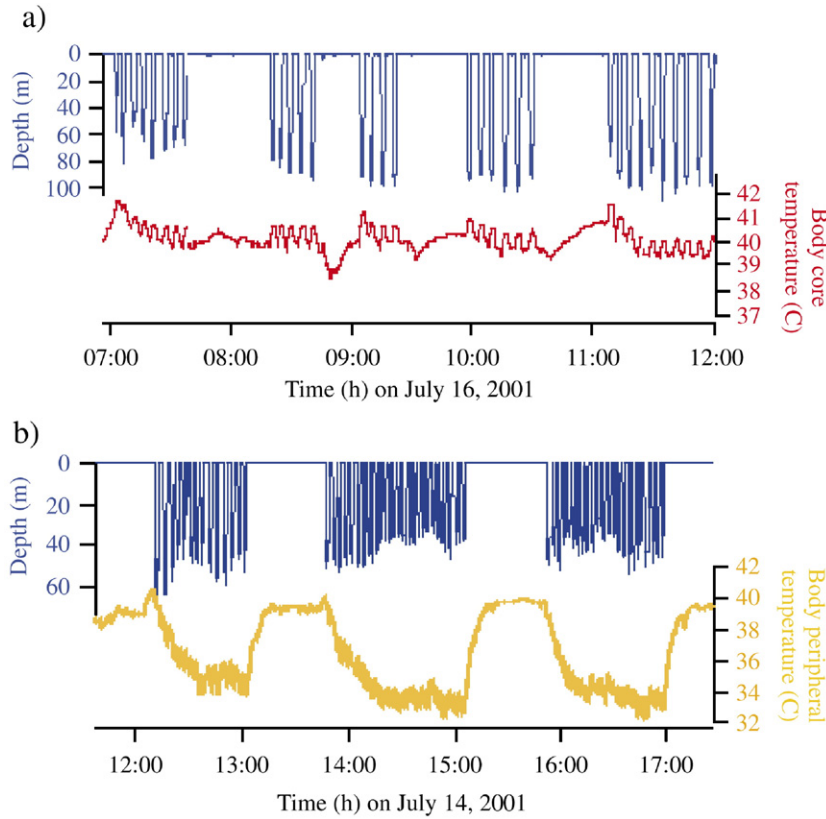
Fig. 3. Temperature changes in (a) body core (T_{bc}) and (b) body periphery (T_{bp}) in response to diving activity in a Brünnich's guillemots. (a) and (b)graphs are T_{bc} and T_{bp}, respectively. The upper and lower lines of the graph represent the diving profiles and body temperatures, respectively. During the diving bouts T_{bc} and T_{bp} decreased as the number of dives increased. However, the average T_{bc} at the end of a dive bout was maintained at similar levels to the birds' resting body temperature.

The incremental change in body temperature (ΔT in °C) while diving could be estimated from the following equation if heat was not lost to the environment from an animal's body:

$$\Delta T = H \cdot (1-0.2)/m \cdot C \tag{1}$$

where H was heat production in Joules (J), C was the heat capacity of the body, and m was body mass in kilograms (Ponganis et al., 1993; Alexander, 1999). It was assumed that metabolic energy efficiency was 20%, heat capacity was 3500 J/kg °C, and the stored oxygen of a 0.9 kg guillemot was 40.32 mL

(Croll et al., 1992). Guillemots could be expected to increase their temperature of whole body by 0.21 °C. We compared the theoretical temperature increase of 0.21 °C to the measured T_{bc} increase in the analysis.

The extent of T_{bc} or T_{bp} changes from the start to the end of each dive was compared to that in subsequent resting periods by using paired t tests. A simple correlation analysis was used in this study because dive depth and duration were significantly correlated ($r=0.77$, $P<0.001$, $r=0.911$, $P<0.001$, $r=0.89$, $P<0.0001$ and $r=0.39$, $P<0.0001$, respectively, for birds #00,

Table 3

Changes in body temperature in core and periphery during diving

Year	ID no.	Number of dive cycles	Changes in T_{bc} or T_{bp} during dives	Changes in T_{bc} or T_{bp} during resting periods	t-value	Degree of freedom	P
Birds recording T_{bc}							
2000	#00	283	0.24±0.20	−0.31±0.20	6.41	282	<0.0001
2001	#L3	571	0.14±0.23	−0.17±0.27	3.94	570	<0.0001
2001	#U2	405	0.01±0.15	−0.07±0.17	7.50	404	<0.0001
Birds recording T_{bp}							
2001	#U30	716	−0.64±0.41	0.58±0.37	4.24	715	<0.0001

Means are given with standard deviation.

Table 4

Mean body temperature of core (T_{bc}) and periphery (T_{bp}) during brooding, and at the start and at the end of dive bouts

Year	ID no.	T_{bc} or T_{bp} during brooding	T_{bc} or T_{bp} at the start of diving bouts	T_{bc} or T_{bp} at the end of diving bouts
Birds recording T_{bc}				
2000	#00	40.0±0.2	40.1±0.4	38.3±0.5
2001	#L3	40.8±0.7	40.7±0.5	39.9±0.7
2001	#U2	39.6±0.2	40.6±0.5	39.6±0.3
Birds recording T_{bp}				
2001	#U30	38.4±0.4	38.8±1.1	35.0±1.0

The sampling year and identification (ID) number of birds are also indicated. Means are given with standard deviation.

L3, U2 and U30). Means ± standard deviations are given in the text.

3. Results

3.1. Dive profile

Guillemots analyzed for T_{bc} in this study made 283–571 dives with a mean duration of 65.5–107.5 s to a mean depth of 12.1–33.7 m (Table 1). The one bird that recorded T_{bp} made 716 dives with a mean duration of 75.1 s to a mean depth of 18.9 m. Birds rested on sea surface for 65.5–107.5 s after a single dive.

Three T_{bc} birds underwent 14–31 dive bouts with a mean duration of 36.6–43.7 min and a single T_{bp} bird made 35 dive bouts with a mean duration of 40.2 min (Table 2). Within a dive bout for T_{bc} birds, there were 15.0–22.9 dives to a mean depth of 12.4–41.9 m. For the one T_{bp} bird, a dive bout had 21.5 dives to a mean depth of 20.4 m.

3.2. Individual dive cycles

Increase in T_{bc} from the start to the end of each dive was significantly higher for deeper dives (Fig. 1a,b,c; $r=0.27$, $P<0.0001$, $r=0.75$, $P<0.0001$, and $r=0.48$, $P<0.0001$, respectively, for birds #00, L3 and U2). Decrease in T_{bc} during subsequent resting periods was significantly lower if subsequent resting period was longer (Fig. 1a,b,c; $r=0.22$, $P<0.001$, $r=0.68$, $P<0.0001$, and $r=0.34$, $P<0.0001$, respectively, for birds #00, L3 and U2). Decrease in T_{bp} from the start to the end of dives was significantly correlated to the dive duration ($r=0.45$, $P<0.0001$) and increases in T_{bp} during subsequent resting period was significantly correlated to the duration for subsequent resting period (Fig. 1d; $r=0.75$, $P<0.0001$). The dives which increased T_{bc}s over 0.21 °C were 47.7, 26.6 and 8.4%, respectively, for birds #00, L3 and U2.

Guillemots increased their T_{bc} rapidly during the ascent dive and slowly during the bottom and descent dives, but decreased during subsequent resting periods between dives (Fig. 2a). Extents of T_{bc} changes during dives were significantly smaller than those during subsequent resting period (Table 3). Contrary to T_{bc}, temperatures in the body periphery decreased at the start of dives, increased during a short period and then decreased after the short period of increase (Fig. 2b). Guillemots overall decreased their T_{bp} during dives, but increased during subsequent resting periods between dives (Fig. 2b). Extents of T_{bp} changes during each dive were significantly greater than those during subsequent resting period (Table 3).

3.3. Dive bouts

Guillemots elevated their body temperature of both core and periphery relatively before engaged sequential dives (Fig. 3a,b). At start of a dive bout T_{bc} of bird #U2 was higher than that for brooding and T_{bc}s of birds #00 and #L3 were similar to those for brooding (Table 4). Guillemots slowly reduced T_{bc} with increasing dive cycles (Fig. 3a). At end of the bout bird #U2 maintained T_{bc} at a slightly higher level than that for brooding but birds #00 and #L3 reduced T_{bc}s at slightly lower levels than those for brooding (Table 4). At the start of a bout T_{bp} (bird #U30) was similar to that of brooding, and decreased largely at the end of a bout (Fig. 3b).

4. Discussion

4.1. Physiological response to dive

Large diving seabirds such as penguins (Spheniscidae) and shags (Phalacrocoracidae) decrease temperatures in their abdominal region or body core (Culik et al., 1996; Bevan et al., 1997; Handrich et al., 1997; Butler, 2000), which probably reduces use of stored oxygen during dives. However, the guillemots in our study could maintain relatively high temperature in body core while adopting the hypothermia only in body periphery. Briefly, the guillemots increased relatively high T_{bc}, but decreased T_{bp} during each dive, whereas they decreased T_{bc} but increased T_{bp} during resting time on sea surface. Although guillemots decreased their temperature in body core in shallower dives, the contrasting change in temperature in body core and periphery is remarkable in deeper dives. This suggests that guillemots have a physiological mechanism to maintain T_{bc} at a high and constant level while diving in cold water, especially during deeper dives.

Considering the contrasting changes in temperatures at the body core and periphery during a single diving cycle, it is likely that peripheral vasoconstriction in blood vessels plays an important role (Scholander et al., 1942; Elsner et al., 1975; Blix and Folkow, 1983; Williams et al., 1999; Boyd, 2000). When the guillemots start a dive, blood probably concentrates in the body core because its perfusion to the periphery is arrested.

4.2. Body temperature and oxygen spare

Concentration of blood to the body core while diving would contribute to maintain an oxygen rich blood supply to vital organs (i.e. breast muscle, heart and brain). Birds could use oxygen stored in the blood effectively for metabolism of vital organs. At the same time, they flap heavily to overcome buoyancy during ascent dive (Watanuki et al., 2003). The high wing beat frequency would necessarily increase heat production (Hindell et al., 2000). Therefore, the restricted blood flow combined with heat production by high wing beat frequency would account for much of heat generation and conservation at the body core region.

Peripheral tissue hypothermia would be expected to reduce metabolic demand through a Q10 effect, thus extending aerobic dive times (Culik et al., 1996; Bevan et al., 1997; Handrich et al., 1997; Butler, 2000). While resting on the sea surface, peripheral vasoconstriction would relax allowing blood flow to the periphery to be restored. Concomitantly, the body core would cool as blood returns from the peripheral tissues. Resumption of breathing after diving would also contribute to heat lost from the body core (Johansen and Bech, 1983; Folkow and Blix, 1987).

Without any effect of the restricted blood flow (see Materials and methods), guillemots could only increase their body temperature by 0.21 °C. However, the measured T_{bc} increases while diving in cold water were often above this value in all three birds (Fig. 1a,b,c). If guillemots restrict blood flow during diving, they would reduce the mass of metabolizable organs and body tissues, which are considered to body core region, by half of the whole body mass as observed by foot-propelled divers (Bevan and Butler, 1992; Stephenson and Jones, 1992). Heat could be conserved only at body core region by the combined effect of restricted blood flow and locomotor activity. As a result, guillemots could increase their temperature at body core by 0.41 °C calculated from Eq. (1) if they inhale oxygen at their theoretical value of 40.32 mL and use it completely. Guillemots could maintain higher temperature in body core while in diving in cold water when adopting restricted blood flow. Consequently, guillemots could achieve the conflict physiological challenge for diving by the combined effects of restricted blood flow and locomotor activity while diving in cold water.

4.3. Body temperature during dive bouts

The brooding guillemots maintained their T_{bc} similar to the range of the birds' resting levels (39.6±0.7 °C, Gabrielsen et al., 1988) although some birds had slightly higher T_{bc} than those for resting ones, which may be related to brooding duties. At the start of a diving bout the birds elevated their T_{bc} higher levels relatively, and they decreased their T_{bc} with increasing dive cycles. The reduction of body core temperature throughout dive bouts arises from large reduction of T_{bc} during the resting time on sea surface but not from the diving time. Similar to T_{bc} guillemot largely reduced their T_{bp} throughout diving bouts. Contrary to T_{bc}, this T_{bp} reduction results from larger reduction of T_{bp} during diving but not from resting on the surface. These changes in body temperature would be a unique physiological response to diving behaviour in small diving birds that is not reported in any large birds diving for longer durations to far deeper depths (Culik et al., 1996; Bevan et al., 1997; Handrich et al., 1997; Butler, 2000). It indicates that regulation of body temperature in small birds could differ from that in large birds.

In conclusion, diving guillemots can conserve body heat at a relatively high level and potentially increase oxygen utilization, as a result of the combined effect of restricted blood flow and high activity level (i.e. wing beat frequency). Overall, this allows the birds to perform as effective predators in cold water.

Acknowledgements

References

Ainley, D.G., Boekelheide, R.J., 1983. An ecological comparison of oceanic seabird communities of the South Pacific Ocean. Stud. Avian Biol. 8, 2–23.

Alexander, R.M., 1999. Energy for animal life. Oxford University Press, New York.

Bevan, R.M., Butler, P.J., 1992. 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., Boyd, I.L., Butler, P.J., Reid, K., Woakes, A.J., Croxall, J.P., 1997. Heart rates and abdominal temperatures of free-ranging south Georgian shags, *Phalacrocorax georgianus*. J. Exp. Biol. 200, 661–675.

Blix, A.S., Folkow, B., 1983. The cardiovascular system. Peripheral circulation and organ blood flow. In: Shepherd, J.T., Abboud, F.M. (Eds.), Handbook of Physiology. Am. Physiol. Soc. pp. 917–945.

Boyd, I.L., 2000. Skin temperatures during free-ranging swimming and diving in Antarctic fur seals. J. Exp. Biol. 203, 1907–1914.

Butler, P.J., 2000. Energetic costs of surface swimming and diving of birds. Physiol. Biochem. Zool. 73, 699–705.

Butler, P.J., Jones, D.R., 1997. Physiology of diving of birds and mammals. Physiol. Rev. 77, 837–899.

Croll, D.A., Gaston, A.J., Burger, A.E., Konnoff, D., 1992. Foraging behavior and physiological adaptation for diving in thick-billed murres. Ecology 73, 344–356.

Culik, B.M., Pütz, K., Wilson, R.P., Bost, C.A., Le Maho, Y., Verselin, J.-L., 1996. Core temperature variability in diving king penguins (*Aptenodytes patagonicus*): a preliminary analysis. Polar Biol. 16, 371–378.

Elsner, R., Hammel, H.T., Heller, H.C., 1975. Combined thermal and diving stresses in the harbor seal *Phoca vitulina*: a preliminary report. Rapp. P.–V. Reun. – Cons. Int. Explor. Mer 169, 437–440.

Folkow, L.P., Blix, A.S., 1987. Nasal heat and water exchange in gray seals. Am. J. Physiol. 253, R883–R889.

Gabrielsen, G.W., Mehlum, F., Karlsen, H.E., 1988. Thermoregulation in four species of arctic seabirds. J. Comp. Physiol. B 157, 703–708.

Gaston, A.J., Jones, I.L., 1998. The Auk. Oxford University Press, New York.

Gentry, R.L., Kooyman, G.L., 1986. Methods of dive analysis. In: Gentry, R.L., Kooyman, G.L. (Eds.), Fur Seals. Princeton University Press, Princeton, pp. 28–40.

Guderley, H., 1990. Functional significance of metabolic responses to thermal acclimation in fish muscle. Am. J. Physiol. 259, R245–R252.

Handrich, Y., Bevan, R.M., Charrassin, J.-B., Butler, P.J., Putz, K., Woakes, A.J., Lage, J., Le Maho, Y., 1997. Hypothermia in foraging king penguins. Nature 388, 64–67.

Hindell, M.A., Lea, M.-A., Morrice, M.G., MacMahon, C.R., 2000. Metabolic limits on dive duration and swimming speed in the southern elephant seal *Mirounga leonina*. Physiol. Biochem. Zool. 73, 790–798.

Johansen, K., Bech, C., 1983. Heat conservation during cold exposure in birds (vasomotor and respiratory implications). Polar Res. 1, 59–268.

Kaseloo, P.A., Lovvorn, J.R., 2005. Effects of surface activity patterns and dive depth on thermal substitution in fasted and fed lesser scaup (*Aythya affinis*) ducks. Can. J. Zool. 83, 301–311.

Kooyman, G.L., Ponganis, P.J., 1998. The physiological basis of diving to depth: birds and mammals. Annu. Rev. Physiol. 60, 19–32.

Lovvorn, J.R., Jones, D., 1994. Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. Estuaries 17, 62–75.

Ponganis, P.J., Kooyman, G.L., 2000. Diving physiology of birds: a history of studies on polar species. Comp. Biochem. Physiol. A 126, 143–151.

Ponganis, P.J., Kooyman, G.L., Castellini, M.A., Ponganis, E.P., Ponganis, K.V., 1993. Muscle temperature and swim velocity profiles during diving in a Weddell seal, *Leptonychotes weddellii*. J. Exp. Biol. 183, 341–348.

Schmidt, A., Alard, F., Handrich, Y., 2006. Changes in body temperatures in king penguins at sea: the result of fine adjustments in peripheral heat loss? Am. J. Physiol. 291, R608–R618.

Scholander, P.F., Irving, I., Grinnell, S.W., 1942. On the temperature and metabolism of the seal during diving. J. Cell. Comp. Physiol. 19, 67–78.

Sibly, R.M., Nott, H.M.R., Fletcher, J., 1990. Splitting behaviour into bouts. Anim. Behav. 39, 63–69.

Stephenson, R., Jones, D.R., 1992. Blood flow distribution in submerged and surface-swimming ducks. J. Exp. Biol. 166, 285–296.

Stonehouse, B., 1967. The general biology and thermal balances of penguins. In: Cragg, J.B. (Ed.), Advances in ecological research. Academic Press, London, pp. 131–196.

Watanuki, Y., Burger, A.E., 1999. Body mass and dive duration in alcids and penguins. Can. J. Zool. 77, 1838–1842.

Watanuki, Y., Mehlum, F., Takahashi, A., 2001. Water temperature sampling by foraging Brunnich's guillemots with bird-borne data loggers. J. Avian Biol. 32, 189–193.

Watanuki, Y., Niizuma, Y., Gabrielsen, G.W., Sato, K., Naito, Y., 2003. Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. Proc. R. Soc. Lond., B 270, 483–488.

Williams, T.M., Noren, D., Berry, P., Estes, J.A., Allison, C., Kirtland, J., 1999. The diving physiology of bottlenose dolphins (Tursiops truncatus) III. Thermoregulation at depth. J. Exp. Biol. 202, 2763–2769.