# THE EFFECTS OF TEMPERATURE ON THE OXYGEN CONSUMPTION, HEART RATE AND DEEP BODY TEMPERATURE DURING DIVING IN THE TUFTED DUCK *AYTHYA FULIGULA*

BY R. M. BEVAN AND P. J. BUTLER

*School of Biological Sciences, The University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK*

## Summary

Six tufted ducks were trained to dive for food at summer temperatures (air, 26°C, water, 23°C) and at winter temperatures (air, 5.8°C, water 7.4°C). The mean resting oxygen consumption ($\dot{V}_{O_2}$) at winter temperatures ($T_{win}$) was 90% higher than that at summer temperatures ($T_{sum}$), but deep body temperatures ($T_b$) were not significantly different.

Diving behaviour and mean oxygen consumption for dives of mean duration were similar at $T_{win}$ and at $T_{sum}$, although the mean oxygen consumption for surface intervals of mean duration was 50% greater at $T_{win}$ and $T_b$ was significantly lower (1°C) at the end of a series of dives in winter than it was in summer.

There appears to be an energy saving of 67 J per dive during winter conditions and this may, at least partially, be the result of the metabolic heat produced by the active muscles being used to maintain body temperature. While at rest under winter conditions, this would be achieved by shivering thermogenesis. Thus, the energetic costs of foraging in tufted ducks in winter are not as great as might be expected from the almost doubling of metabolic rate in resting birds.

## Introduction

During the winter, most homeotherms maintain a high body temperature despite low ambient temperatures. This they are able to achieve through physiological, behavioural and morphological adjustments (Calder and King, 1974). For semi-aquatic homeotherms (e.g. ducks, penguins and muskrats), the maintenance of body temperature is especially difficult because of the high thermal conductivity and heat capacity of water (the conductivity of water is approximately 24 times greater than that of air). Consequently, heat loss in water is much higher than that in air at equivalent temperatures (Holmer and Bergh, 1974; Kooyman *et al.* 1976; Grant and Dawson, 1978; Dawson and Fanning, 1980; Stahel and Nicol, 1982; Barre and Roussel, 1986; Jenssen *et al.* 1989), despite the

fact that a boundary layer of air is normally retained, even in swimming birds (Rijke, 1970).

An additional factor that can affect heat loss, since it will increase the convection of heat from a body, is movement (Calder and King, 1974). This heat loss will be even greater in water (MacArthur, 1984; Williams, 1986). Furthermore, by moving, the effectiveness of many of the behavioural mechanisms for maintaining body temperature [e.g. by reducing the body surfaces exposed to the environment (Calder and King, 1974) or by changing posture (Webster, 1985)] will be reduced or even lost. Heat loss from moving limbs, however, can be reduced through a countercurrent exchange of heat between the arteries and veins of the legs (Kahl, 1963; Steen and Steen, 1965).

Diving birds will be presented with an even greater challenge to the maintenance of body temperature, since they will be completely surrounded by the cold water. Moreover, the hydrostatic pressure experienced by an animal during a dive can force air from the insulation layer (feathers or hair) (Kooyman et al. 1976; Stephenson et al. 1988), thus reducing the insulating properties of this layer. The increased metabolic rate of the working muscles of an actively diving animal, however, will increase heat production and may compensate for the elevated heat loss (Paladino and King, 1984). It is a matter of debate whether this exercise-generated heat is sufficient to counter-balance the heat loss (Schuchmann, 1979; Paladino and King, 1984; Webster and Weathers, 1990).

During diving, a further restrictive factor is the limited supply of oxygen that an animal can utilise. In the tufted duck, diving for normal durations (15–20 s) can be energetically as costly as swimming at maximum sustainable swimming speed (Woakes and Butler, 1983). Any increase in the oxygen consumption for thermogenesis (possibly through the shivering action of the pectoral muscles) will, therefore, decrease the duration that the bird can remain submerged whilst still metabolising aerobically.

Diving birds are, therefore, faced with a number of strategies when diving in cold water: (1) do they increase their metabolic rate and maintain body temperature whilst depleting the oxygen stores at a faster rate, (2) do they conserve the oxygen stores and allow the body temperature to fall, or (3) do increases in the insulation warrant no adjustment to the physiology?

The objective of this study was to determine whether the 'wasted' energy (heat) of locomotion is used for thermoregulation by measuring the oxygen consumption, heart rate and body temperature during diving activity of tufted ducks acclimated to summer and winter temperatures.

## Materials and methods

Six tufted ducks (*Aythya fuligula*, L.), of either sex, were used to determine the effects of temperature on the energetic costs of diving. The ducks had a mean body mass of 578±25 g and 605±11 g at the summer and winter temperatures,

respectively. They were kept separately in indoor tanks (0.6 m×0.6 m×1.0 m; water depth 0.6 m) where they were trained to dive in response to a series of computer-controlled lights (Bevan *et al.* 1992). The electrocardiogram (ECG) and deep body temperature of the birds were monitored *via* a pulse-interval-modulated radiotransmitter (Woakes, 1980) implanted under halothane anaesthesia into the abdominal cavity of each bird (for implantation procedure, see Stephenson *et al.* 1986). When the birds were fully recovered, training was recommenced. The light schedule was held at 12 h:12 h L:D to eliminate any effect of differing light intensities on the acclimation process and on the metabolic rate. The water and air temperatures were not controlled during the periods prior to acclimation but fluctuated with ambient temperature, thus facilitating the acclimation process.

When they had been trained to dive for durations of approximately 20 s, the ducks were acclimated to summer temperatures during July–September 1988. Acclimation entailed housing the ducks in the training tanks, and heating the water supply with an in-line water heater (Heatrae Industrial Ltd). Air temperature was within 1 °C of the water temperature during the acclimation period. The birds were acclimated over a period of at least 3 weeks before any measurements were taken, during which they were trained to dive from a respirometer box (Bevan *et al.* 1992). Oxygen consumption and carbon dioxide production were measured as in Woakes and Butler (1983). Over any period of measurement, the temperature of the air rose above that of the water because of the heat produced by the mass spectrometer; consequently, the air temperature was 26.4±0.5 °C (mean±S.E.), as opposed to 22.9±0.4 °C for that of the water. The signal from the implanted transmitter was detected by a receiver (Sony 5090) and sent through a purpose-built decoder (Woakes, 1980) to extract the ECG. Heart rate was obtained by passing the ECG through an instantaneous rate meter (Devices Ltd). Deep body temperature was also monitored as the frequency of the signal from the transmitter is directly proportional to temperature. The concentrations of oxygen and carbon dioxide, ECG and heart rate were recorded on a four-channel pen recorder with rectilinear coordinates (Lectromed Ltd). Measurements from each bird were obtained whilst diving over a 3 h period on at least 3 days.

Winter temperatures were achieved by transferring the system to a constant-temperature room, where the air temperature was held at 5.8±0.5 °C. The temperature of the water entering the room was not controlled but, by performing the experiments in the winter months (December 1988 to April 1989), the mean water temperature was kept low (7.4±0.1 °C). Again, $O_2$ and $CO_2$ concentrations within the respirometer, ECG, heart rate and deep body temperature were monitored during diving. Ducks that had been acclimated to the summer temperatures were also acclimated to the winter ones, allowing a direct comparison to be made between the responses to the different temperatures.

The transmitters were calibrated for temperature both before and at the end of the experiments (after the transmitters had been removed from the birds under general anaesthesia). Calibration entailed placing the transmitter in a water bath

and monitoring the pulse frequency of the signal over the 36–44°C temperature range.

The traces of the oxygen and carbon dioxide concentration and of heart rate were digitised using a digitizer (GTCO Digipad 5, S.S.I. Ltd) connected to microcomputer (BBC Model B). The technique of Woakes and Butler (1983) was employed to estimate the oxygen consumption during submersion and during the surface intervals (Bevan et al. 1992).

Values are given as the means±S.E. A paired $t$-test was used to determine any statistical difference between two means, tested at the 95 % level ($P<0.05$), using the MINITAB statistical package. The number of observations ($N$) was six in all cases, and the overall mean values were derived from the mean data obtained from each individual duck. $T_{win}$ represents the winter temperatures and $T_{sum}$ the summer temperatures.

## Results

### Resting values

Table 1 contains data obtained from resting birds that were floating quietly on the surface of the water. The mean resting oxygen consumptions of the summer-acclimated birds ranged from 0.097 to 0.218 ml s$^{-1}$ whereas the winter-acclimated animals had mean resting oxygen consumptions ranging from 0.251 to 0.399 ml s$^{-1}$. The mean resting oxygen consumption at $T_{win}$ was 90 % higher than that at $T_{sum}$ ($t=-9.13$; $P=0.0003$). The mean resting carbon dioxide production of the six birds followed the same pattern as oxygen consumption, and was higher at $T_{win}$ (0.242±0.025 ml s$^{-1}$) than at $T_{sum}$ (0.155±0.027 ml s$^{-1}$). The respiratory exchange ratio (RE), though lower at $T_{win}$, was not significantly different from that at $T_{sum}$. Heart rate at rest was significantly different at the two ambient temperatures. The values from individual birds ranged from 96 to 135 beats min$^{-1}$ at $T_{sum}$ and from 143 to 167 beats min$^{-1}$ at $T_{win}$. The deep body temperatures of

Table 1. *Mean values of gas exchange and heart rate obtained from six tufted ducks resting on water under winter and summer conditions*

| | Summer | Winter |
|---|---|---|
| Mass (kg) | 578±25 | 605±11 |
| Water temperature (°C) | 22.9±0.4 | 7.4±0.1*** |
| Air temperature (°C) | 26.4±0.5 | 5.8±0.5*** |
| Heart rate (beats min$^{-1}$) | 112.0±6.7 | 150.2±5.3** |
| Oxygen consumption (ml s$^{-1}$) | 0.175±0.019 | 0.333±0.020*** |
| Carbon dioxide production (ml s$^{-1}$) | 0.155±0.027 | 0.242±0.025* |
| Respiratory exchange ratio | 0.86±0.09 | 0.75±0.13 |

Values given are the means±S.E.

Significant differences between the summer and winter values, obtained from a paired $t$-test, are represented by an asterisk: * $P>0.05$; ** $P>0.01$; *** $P>0.001$.
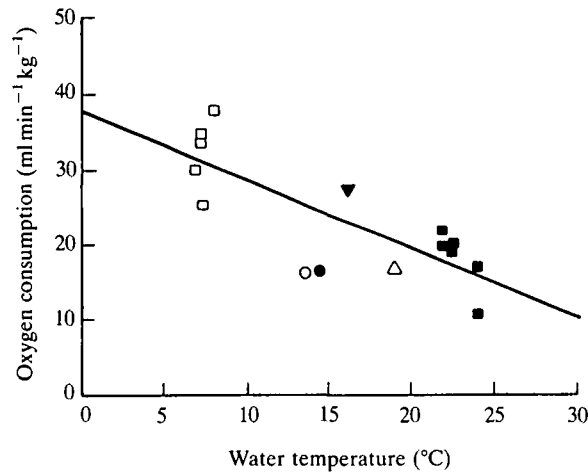
Fig. 1. Diagram showing the correlation between water temperature and resting oxygen consumption in tufted ducks. Values are from birds resting on the water surface. The relationship is described by the equation: $\dot{V}_{O_2} = 37.83 - 0.916 T_w$, $r^2 = 0.61$, where $\dot{V}_{O_2}$ is oxygen consumption in $\mathrm{ml\,min^{-1}\,kg^{-1}}$ and $T_w$ is water temperature in °C. (□) Mean values from the birds held at winter temperatures; (■) means from the same birds held at summer temperatures; (○) and (●) means from the data of Woakes and Butler (1983), (△) from Butler *et al.* (1988) and (▼) from Bevan *et al.* (1992).

the resting animals were not significantly different at the two temperatures (see Fig. 2).

Incorporating data from the present and previous studies (Woakes and Butler, 1983; Butler *et al.* 1988; Bevan *et al.* 1992), resting oxygen consumption was found to be inversely related to water temperature (Fig. 1). The relationship between the two variables is described by the equation:

$$y = 37.83(\pm 0.44) - 0.916(\pm 0.048)x, \qquad r^2 = 0.61,$$

where $y$ is oxygen consumption in $\mathrm{ml\,min^{-1}\,kg^{-1}}$ and $x$ is water temperature in °C.

## The effects of diving

Several of the variables measured during diving are given in Table 2. There were no significant differences in dive duration ($t_d$), surface interval duration (the time spent at the surface between dives, $t_i$) or in the duration of the total dive cycle (the time spent performing a dive plus the succeeding time spent on the surface, $t_c$) measured at $T_{sum}$ and $T_{win}$. The total amount of oxygen consumed over $t_c$ was approximately 35 % higher at $T_{win}$, and, since $t_c$ was slightly shorter, the rate of oxygen consumption over the total dive period was 43 % higher at $T_{win}$ than at $T_{sum}$ ($t = -5.38$, $P = 0.003$).

The average oxygen consumption during submersion ($\dot{V}_{O_2d}$) and that during the surface intervals ($\dot{V}_{O_2i}$) was estimated using a linear multiple regression. The partial correlation coefficients of the estimated $\dot{V}_{O_2d}$ ranged from 0.52 to 0.80

Table 2. *Mean values of gas exchange, body temperature, heart rate and behaviour obtained during diving from six tufted ducks acclimated to summer and winter temperatures (see Table 1)*

| | Summer | Winter |
|---|---|---|
| Dive duration, $t_d$ (s) | 18.9±0.9 | 16.2±0.8 |
| Surface interval duration, $t_i$ (s) | 11.6±1.1 | 12.8±1.6 |
| Duration of total dive cycle, $t_c$ (s) | 30.5±1.2 | 29.0±2.3 |
| Total oxygen consumed over a dive cycle (ml) | 12.1±0.9 | 16.4±1.0* |
| Deep body temperature (°C) | 41.5±0.2 | 40.5±0.4* |
| Average oxygen consumption during submersions of mean duration, $t_d$, $\dot{V}_{O_2d}$ (mls$^{-1}$) | 0.400±0.032 | 0.349±0.034 |
| Average oxygen consumption during surface intervals of mean duration, $t_i$, $\dot{V}_{O_2i}$ (mls$^{-1}$) | 0.353±0.043 | 0.526±0.038* |
| Oxygen consumption over total dive cycle (mls$^{-1}$) | 0.397±0.028 | 0.568±0.016** |
| Heart rate over total dive cycle (beats min$^{-1}$) | 189±11 | 224±13* |

Values given are the means±S.E.

Significant differences between the summer and winter values, obtained from a paired $t$-test, are represented by an asterisk: * $P>0.05$; ** $P>0.01$.

(mean 0.68±0.04) and those for $\dot{V}_{O_2i}$ from 0.64 to 0.81 (mean 0.66±0.03). All the regressions were highly significant ($P<0.001$). From this analysis, it was found that there was no significant difference between $\dot{V}_{O_2d}$ at the two temperature regimes ($t=1.21$, $P=0.28$), whereas $\dot{V}_{O_2i}$ at $T_{win}$ was 50% greater than it was at $T_{sum}$ ($t=-4.30$, $P=0.013$) (Table 2). This difference was seen regardless of the fact that $t_d$ and $t_i$ were not significantly different at the two temperatures.

Even though the body temperatures at rest were similar at $T_{sum}$ and $T_{win}$, the body temperature during diving activity (taken at the end of a diving bout) was elevated at $T_{sum}$, but was depressed at $T_{win}$ (Fig. 2). Although each was not significantly different from the corresponding resting value, there was a significant difference between the two values of mean deep body temperature during diving ($t=3.41$, $P=0.019$).

The diving heart rate was measured over the last 5s of a dive (but excluded the data over the 1s prior to surfacing, where anticipatory changes can occur). This range was chosen as it can be indicative of other physiological adjustments that may be occurring (Stephenson *et al.* 1986). Heart rate during diving was 60% greater than that in the resting animal at $T_{sum}$, although it was only 40% greater than that at rest at $T_{win}$ (Fig. 3). However, the rates during diving at the two temperatures were not found to be significantly different from each other ($t=1.95$, $P=0.15$). Mean heart rate over the total dive cycle was 20% higher at $T_{win}$ than at $T_{sum}$ (Table 2), and reflected the overall increase in metabolism during diving activity at $T_{win}$.

## Discussion

The aim of the present study was to determine how diving birds adjust their

energetic demands at different environmental temperatures. Most studies on the responses of birds to different ambient temperatures have concentrated on air temperature (Bech, 1980; Bucher, 1981; Chappell and Bucher, 1987; Stahel *et al.* 1987; Gabrielsen *et al.* 1988; Webster and Weathers, 1988; Chappell *et al.* 1989). Very few studies have looked at the energetic costs of resting at various water
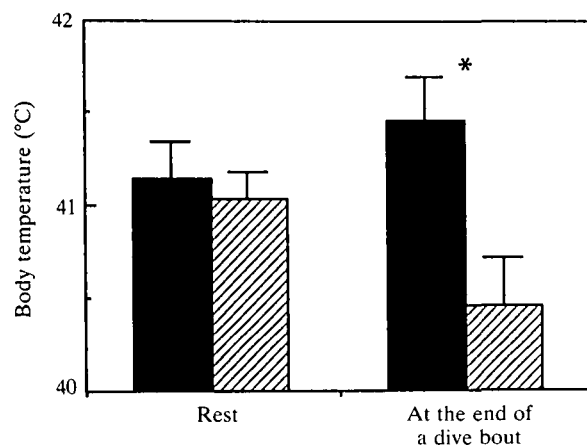


Fig. 2. Histogram showing mean values of deep body temperature in six tufted ducks acclimated to summer (■) or winter (▨) temperatures while at rest and at the end of a diving bout. The bar above each column is +1 s.e. and an asterisk indicates a significant difference ($P<0.05$) between the relevant summer and winter values.
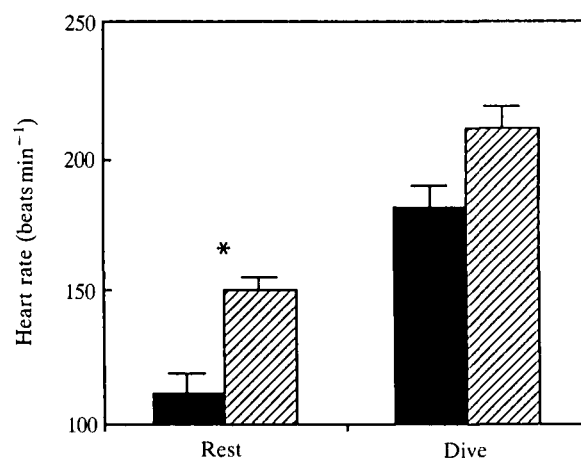


Fig. 3. Mean heart rates in six tufted ducks acclimated to summer (■) or winter (▨) temperatures while at rest and during the final 5 s of a dive (excluding the data during the last second before surfacing). The bar above each column is +1 s.e. and an asterisk indicates a significant difference ($P<0.05$) between the relevant summer and winter values.

Table 3. *The relationship between resting oxygen consumption ($ml\,O_2\,min^{-1}$ $kg^{-1}$; y) and water temperature (°C; x) for several avian species; the relationship is of the form:* y=ax+b

| Species | a | b | Reference |
|---|---|---|---|
| Adélie penguin *Pygoscelis adeliae* | −1.291 | 53.54 | Kooyman *et al.* (1976) |
| Macaroni penguin *Eudyptyla chrysolophus chrysolophus* | −1.606 | 64.62 | Barre and Roussel (1986) |
| King penguin *Aptenodytes patagonicus* | −0.591 | 29.15 | Barre and Roussel (1986) |
| Eider duck *Somateria mollissima* | −0.273 | 16.60 | Jenssen *et al.* (1989) |
| Tufted duck *Aythya fuligula* | −0.916 | 37.83 | Present study |

The data for the macaroni and king penguins were converted from $W\,kg^{-1}$ to $ml\,O_2$ $min^{-1}\,kg^{-1}$ using the conversion factor $3.030\,W\,kg^{-1}$ is equivalent to $1\,ml\,O_2\,min^{-1}\,kg^{-1}$ (Jenssen *et al.* 1989).

temperatures, despite the large increase in thermal conductance and the reduction of insulation (Kooyman *et al.* 1976; Jenssen *et al.* 1989). In addition, no other study has looked at the effect of movement in water on the thermogenic response of birds, even though this has been shown to have a marked effect in mammals (Nadel *et al.* 1974; MacArthur, 1984; Williams, 1986).

It would appear that the resting tufted duck does not reduce its energy costs in winter by reducing its body temperature (and hence the heat gradient between itself and the external environment) during the day, as some other birds do (Bech, 1980; Rintmaki *et al.* 1983; Groscolas, 1986; Jenssen *et al.* 1989). However, the ducks may have had a reduced body temperature, and hence reduced energy demands, during the night (cf. Reinertsen and Haftorn, 1986).

The twofold increase in the resting oxygen consumption of ducks exposed to low water temperatures was no doubt due to an increase in the metabolic heat production needed to maintain body temperature. This is not surprising in a semi-aquatic bird, since simply resting on water causes the conductance of the feather/air layer to increase (Stahel and Nicol, 1982; Kooyman *et al.* 1976). The relationship found between the resting mass-specific oxygen consumption and the ambient water temperature is in agreement with other studies performed on a variety of avian species (Table 3). The increased metabolic rate of the tufted ducks at $T_{win}$ is sufficient to maintain deep body temperature at the same level as that at $T_{sum}$.

The body temperature of some diving animals has been shown to decrease during diving (Scholander *et al.* 1942; Kooyman *et al.* 1980; MacArthur, 1984), although it can increase (Stephenson, 1987) or remain unchanged in others (Gallivan and Roland, 1979). The drop in body temperature of the muskrat was found to be a function of both water temperature and dive duration (MacArthur, 1984). In the tufted duck, the body temperature has been shown to increase during swimming (Woakes and Butler, 1983) and whilst diving (Stephenson, 1987). When swimming on water at a temperature of 17.8°C and consuming oxygen at the same

rate as that during diving, tufted ducks show an increase in body temperature of approximately 0.5 °C (Woakes and Butler, 1983).

As $t_d$, $t_i$ and $t_c$ were all similar under the two conditions (summer and winter), the differences that were discovered between the physiological responses to diving at $T_{win}$ and $T_{sum}$ must have been due to the temperature differences. In the present study, the deep body temperature during diving at $T_{sum}$ also increased, but at $T_{win}$ it was reduced. As $\dot{V}_{O_2d}$ was not significantly different at the two temperatures, it would appear that the ducks allow their body temperature to fall when diving in cold water rather than increasing heat production by using up the limited oxygen stores. Indeed, $\dot{V}_{O_2i}$ at $T_{win}$ is 50 % greater than that at $T_{sum}$, probably because the birds increase thermogenesis when they are at the surface and have free access to air.

It should be noted that $\dot{V}_{O_2d}$ is not necessarily the rate that occurs throughout the dive. Bevan *et al.* (1992) found that, for a group of birds, $\dot{V}_{O_2d}$ was lower in the birds that had the longer mean dive durations, with $\dot{V}_{O_2d}$ declining as mean dive duration increased (at a rate of $-0.019$ ml $O_2$ per second of dive duration).

The oxygen consumption over $t_c$ at $T_{win}$ is 43 % greater than it is at $T_{sum}$, but this is considerably less than the 90 % increase found in the resting birds. This suggests that the heat generated by the active muscles during diving compensates, at least partially, for the heat loss, and will serve as a way in which the foraging costs of these birds can be kept to a minimum (cf. Webster and Weathers, 1990). However, a lower body temperature while diving during winter may also benefit the birds in that a reduction in the temperature of the tissues will decrease the rate at which oxygen is consumed, so prolonging the potential maximum aerobic dive duration.

The rate of aerobic energy consumption that can be attributed solely to the act of diving can be calculated as the average rate at which energy is consumed over the mean dive duration $(0.40 \, \text{ml} \, O_2 \, \text{s}^{-1})$ minus the mean resting value $(0.17 \, \text{ml} \, O_2 \, \text{s}^{-1})$, both obtained at $T_{sum}$. This rate of aerobic metabolism during diving $(0.23 \, \text{ml} \, O_2 \, \text{s}^{-1})$ should remain constant regardless of the water temperature, given that all other factors, such as water depth and dive duration, remain constant. Consequently, the overall rate of energy consumption during diving at $T_{win}$ should equal the resting oxygen consumption at $T_{win}$ plus the aerobic cost of diving $(0.33+0.23=0.56 \, \text{ml} \, O_2 \, \text{s}^{-1})$. This is $0.21 \, \text{ml} \, O_2 \, \text{s}^{-1}$ more than the measured value, and is equivalent to an average saving of $3.4 \, \text{ml} \, O_2$ per dive or 67 J (using $19.80 \, \text{J} = 1 \, \text{ml} \, O_2$; Jenssen *et al.* 1989). For the tufted ducks, this reduction in the cost of foraging could be an important factor in the survival of the animal, especially when food supplies are low.

There is evidence to suggest that other aquatic animals use the metabolic heat produced by activity to maintain body temperature during diving. The oxygen uptake of Weddell seals whilst diving is 82 % of that recorded whilst resting in the water (Kooyman *et al.* 1973), and the oxygen uptake of foraging king penguins has been estimated to be 74 % of the calculated resting oxygen consumption (Butler and Jones, 1982). Thus, at low temperatures, thermoregulatory heat production may be largely substituted by the heat produced by the active muscles. Although

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this does not occur in flying hummingbirds (Schuchmann, 1979), it would be a useful way for active homeotherms to keep the energy costs of foraging to a minimum (Bevan and Butler, 1989).

In an earlier study of the tufted duck (Bevan et al. 1992), it was found that heart rate could be a very good indicator of oxygen consumption over a dive cycle, as it is in other aquatic animals (Fedak et al. 1988; Williams et al. 1991). The applicability of this relationship was tested again in the present study. The mean $\dot{V}_{O_2}$ predicted

Table 4. *Comparison of measured oxygen consumption with that predicted from heart rate*

| | Measured | | Predicted $\dot{V}_{O_2}$ (ml s$^{-1}$) | Percentage error |
|---|---|---|---|---|
| | Heart rate (beats min$^{-1}$) | $\dot{V}_{O_2}$ (ml s$^{-1}$) | | |
| Rest at | | | | |
| $T_{sum}$ | 112 | 0.175 | 0.173 | −1.1 |
| $T_{win}$ | 150 | 0.333 | 0.298 | −10.5 |
| Total dive cycle at | | | | |
| $T_{sum}$ | 189[a] | 0.397 | 0.425 | 7.1 |
| $T_{win}$ | 224[a] | 0.568 | 0.540 | −4.9 |

The equation used to predict oxygen consumption was obtained from the data of Woakes and Butler (1983) for swimming birds: $y=0.00327x-0.193$, where $y$ is oxygen consumption and $x$ is heart rate.

[a] Heart rate measured over the total dive cycle.

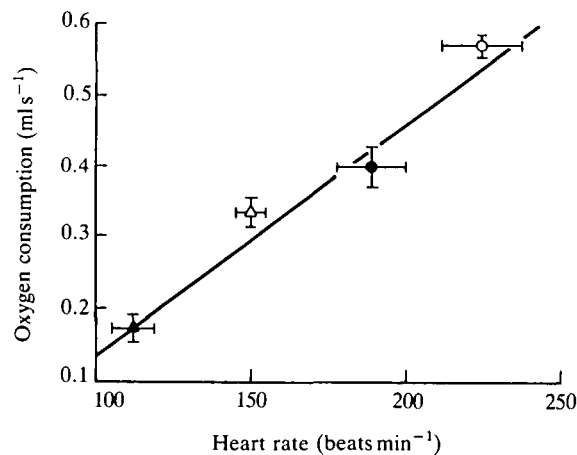$T_{sum}$, values at summer temperatures; $T_{win}$, values at winter temperatures.



Fig. 4. The relationship between mean heart rate and mean oxygen consumption (±S.E.) of tufted ducks at rest (▲) and over the total dive cycle (●) at summer temperatures, and at rest (△) and over the total dive cycle (○) at winter temperatures. Also plotted is the regression line of oxygen consumption against heart rate from swimming tufted ducks (Woakes and Butler, 1983).

from the mean heart rates whilst at rest and over a total dive cycle (using the equation of Woakes and Butler, 1983) were found to be in excellent agreement with the direct measurements (Table 4 and Fig. 4). This demonstrates still further the usefulness of heart rate as an indicator of oxygen metabolism in this species (Bevan *et al.* 1992).

The present study has been able, in part, to elucidate the metabolic response of tufted ducks to the harsh thermal conditions of a cold aquatic environment. However, in the wild, the metabolic response may differ as a result of other factors, e.g. wind-induced convection. Also, the birds in the present study were well fed, whereas in the wild there might well be a scarcity of food material, which could have an effect on the thermogenic response. Reduced food availability may stimulate the birds to reduce the rate at which the body stores are used, and this could be achieved by reducing the body temperature (Groscolas, 1986).

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