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Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*)

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Summary

Diving is believed to be very costly in cormorants (Phalacrocoracidae) when compared with other avian divers because of their poor insulation and less-efficient foot propulsion. It was therefore suggested that cormorants might employ a behavioural strategy to reduce daily energy expenditure by minimizing the amount of time spent in water. However, European shags (*Phalacrocorax aristotelis*) have been observed to spend up to 7 h day^{-1} diving in water of around 5–6°C. To gain a better understanding of the energetic requirements in European shags, we measured their metabolic rates when resting in air/water and during shallow diving using respirometry. To investigate the effects of water temperature and feeding status on metabolic rate, birds dived at water temperatures ranging from 5 to 13°C in both post-absorptive and absorptive states. In parallel with respirometry, stomach temperature loggers were deployed to monitor body temperature. Basal metabolic rate (*BMR*) was almost identical to allometric predictions at 4.73 W kg^{-1}. Metabolic rate when resting on water, during diving and after feeding was significantly elevated when compared with the resting-in-air rate. During diving, the metabolic rate of post-absorptive shags increased to 22.66 W kg^{-1}, which corresponds to 4.8× *BMR*. Minimum cost of transport (*COT*) was calculated at 17.8 J kg^{-1} m^{-1} at a swim speed of 1.3 m s^{-1}. Feeding before diving elevated diving metabolic rate by 13% for up to 5 h. There was a significant relationship between diving metabolic rate and water temperature, where metabolic rate increased as water temperature declined. Thermal conductance when resting in air at 10–19°C was 2.05 W m^{-2} °C^{-1} and quadrupled during diving (7.88 W m^{-2} °C^{-1}). Stomach temperature when resting in air during the day was 40.6°C and increased during activity. In dive trials lasting up to 50 min, stomach temperature fluctuated around a peak value of 42.0°C. Hence, there is no evidence that European shags might employ a strategy of regional hypothermia. The energetic costs during shallow diving in European shags are considerably lower than has previously been reported for great cormorants (*Phalacrocorax carbo*) and are comparable to other foot-propelled divers. The lower dive costs in shags might be the consequence of a more streamlined body shape reducing hydrodynamic costs as well as a greater insulative plumage air layer (estimated to be 2.71 mm), which reduces thermoregulatory costs. The latter might be of great importance for shags especially during winter when they spend extended periods foraging in cold water.

Key words: metabolism, diving, thermoregulation, European shag, *Phalacrocorax aristotelis*, energetics, HIF.

Introduction

Seabirds face an energetically challenging situation when diving in cold water. As homeotherms, avian divers regulate their body temperature within a narrow range, with core body temperatures typically between 38 and 42°C (Dawson and Whittow, 2000). Water has a heat capacity 4000 times greater than that of air and a thermal conductivity 25 times that of air. Hence, cold water is an enormous heat sink. Unless properly insulated, birds will lose heat very rapidly in cold water, and the thermoregulatory costs might be a great burden to the overall energy budget. Although a body of information on the diving energetics of wing-propelled divers (especially penguins) has emerged in recent years (for a review, see Ellis and Gabrielsen, 2002), measurements of diving costs for foot-propelled divers are scarce. Apart from diving ducks, the only foot-propelled pursuit divers that have been investigated are the two sub-species of the great cormorant (*Phalacrocorax carbo sinensis* – Schmid et al., 1995; *Phalacrocorax carbo carbo* – Grémillet et al., 2001, 2003), while Ancel et al. (2000) investigated the metabolic rate of Brandt's cormorants (*Phalacrocorax penicillatus*) during surface swimming.

Great cormorants and European shags (*Phalacrocorax aristotelis*) are foot-propelled pursuit divers that forage on benthic and pelagic fish, which they catch inshore. Both species range from mild temperate climatic zones to thermally

challenging arctic zones (Johnsgard, 1993). The plumage of shags and cormorants is supposedly wettable (Rijke, 1968), and the plumage air volume is reduced when compared with other aquatic birds (Wilson et al., 1992; Grémillet et al., 2005), reducing buoyancy. Buoyancy is the dominant factor determining dive costs in lesser scaup ducks (*Aythya affinis*; Stephenson, 1994); hence, a reduction in buoyancy will tend to reduce dive costs. However, unlike in penguins, the subcutaneous fat layer of shags and cormorants is negligible and they have to rely on plumage air as an insulating layer when diving in cold water. A thinner insulating layer will make them prone to heat loss; hence, it is not surprising that cormorants and shags leave the water at the end of a foraging bout to rest on land.

Schmid et al. (1995) measured the diving metabolic rate of great cormorants (*P. c. sinensis*) as ~10–12 times their metabolic rate when resting in air (*RMR*). This is in strong contrast to the diving metabolic rates that have been reported for other diving birds, which typically range between two and four times basal metabolic rate (*BMR*) for wing-propelled divers and between three and five times *BMR* for foot-propelled divers (see Table 1). Schmid et al. (1995) attributed these exorbitant costs to the poor insulation of cormorants (supposedly wettable plumage) and the less efficient mode of propulsion (drag-based oscillations, generating thrust only during one phase of the cycle) when compared with wing-propelled divers (lift-based oscillations, generating thrust during both phases of the cycle; Lovvorn, 2001; Lovvorn et al., 2004). However, Johanssen and Norberg (2003) showed that, instead of relying entirely on drag-based propulsion, great cormorants (and probably most foot-propelled divers) use a combination of drag-based and lift-based propulsion during diving, increasing hydrodynamic and, hence, energetic efficiency. Similarly, Grémillet et al. (2001) used a model integrating the effect of water temperature and dive depth on energy expenditure during diving to estimate the energetic costs of foraging great cormorants (*P. c. carbo*) in Greenland and France. They calculated that dive costs will vary between nine and 21 times *RMR* (Schmid et al., 1995) when diving in shallow/warm water and deep/cold water, respectively.

These high energy costs during foraging contrast with the finding by Grémillet et al. (2003) that daily food requirements

Table 1. *Metabolic rates of foot-propelled and wing-propelled avian divers when resting in air and water and during diving*

Species	Mass (kg)	Water temp. (°C)	*BMR** (W kg^{-1})	Resting in water† (W kg^{-1})	(× *BMR*)	Diving (W kg^{-1})	(× *BMR*)	Source
Foot-propelled divers								
Aythya fuligula (*Af*)	0.597	13.6	4.80	5.38	1.1	18.68	3.9	Woakes and Butler (1983)
	0.578	23.0	4.80	5.96	1.2	13.53	2.8	Bevan and Butler (1992)
	0.571	14.4	4.80	7.52	1.6	15.21	3.2	Bevan et al. (1992)
	0.605	7.4	4.80	10.84	2.3	18.50	3.8	Bevan and Butler (1992)
	0.600	22.0	4.80	5.83	1.2	19.00	4.0	De Leeuw (1996)
	0.600	8.0	4.80	8.33	1.7	24.50	5.1	De Leeuw (1996)
Aythya affinis (*Aa*)	0.591	13.0	4.80	7.90	1.6	21.00	4.4	Stephenson (1994)
Somateria mollissima (*Sm*)	1.79	13.7–19.0	4.20	10.05	2.4	16.09	3.8	Hawkins et al. (2000)
Phalacrocorax carbo (*Pc*)	2.40	12.6	3.10	14.10	4.5	31.40	10.1	Schmid et al. (1995)
Phalacrocorax carbo (*Pc*)	2.54	5.1	3.10	14.10	4.5	29.10	9.4	Grémillet et al. (2003)
Phalacrocorax aristotelis (*Pa*)	1.67	9.0	4.73	19.37	4.1	22.66	4.8	Present study
Wing-propelled divers								
Uria lomvia (*Ul*)	0.803	20.0	8.59	8.84	1.0	21.17	2.5	Croll and McLaren (1993)
Uria aalge (*Ua*)	0.836	20.0	7.18	7.30	1.0	16.51	2.3	Croll and McLaren (1993)
Eudyptula minor (*Em*)	1.20	21.0	3.30	6.40	1.9	7.28	2.2	Baudinette and Gill (1985)
Eudyptula minor (*Em*)	1.20	10.0	3.30	8.50	2.6	12.90	3.9	Bethge et al. (1997)
Spheniscus humboldti (*Sh*)	4.60	18.0	2.45	4.25	1.7	7.24	3.0	Butler and Woakes (1984)
Spheniscus humboldti (*Sh*)	3.60	19.0	2.45	5.95	2.4	10.20	4.2	Luna-Jorquera and Culik (2000)
Pygoscelis antarctica (*Pan*)	3.80	4.0	3.72	8.75	2.3	8.90	2.4	Culik et al. (1994)
Pygoscelis adeliae (*Pad*)	4.00	4.0	3.72	8.36	2.2	10.80	2.9	Culik et al. (1994)
Pygoscelis papua (*Pp*)	5.50	4.0	3.89	8.19	2.1	13.70	3.5	Culik et al. (1994)
Aptenodytes patagonicus (*Ap*)	11.50	9.1	3.50	4.65	1.3	8.40	2.4	Culik et al. (1996)
Aptenodytes forsteri (*Afo*)	23.30	1.5–6.1	1.98	2.14	1.1	6.57	3.3	Kooyman and Ponganis (1994)

Only respirometry studies were included in Table 1. An energetic equivalent of 19.7 kJ l^{-1} O_2 was assumed when transforming oxygen consumption to Watts.

*Basal metabolic rate (*BMR*) values were taken from the following sources: *Af* and *Aa*, Daan et al. (1990); *Pc*, Schmid et al. (1995); *Em*, Stahel and Nicol (1988); *Sh*, Drent and Stonehouse (1971); *Pan* and *Pad*, Chappell and Souza (1988); *Pp*, Bevan et al. (1995); *Ap*, Cherel et al. (1988); *Afo*, Le Maho et al. (1976).

†Resting-in-water rates were taken from Schmid et al. (1995) for *Pc* and from Culik et al. (1991) for *Pan*, *Pad* and *Pp*.

in cormorants are normal for a seabird of its mass. Hence, it was suggested that cormorants might employ a behavioural strategy whereby birds will minimize the amount of time spent in the water to reduce daily energy expenditure, especially when wintering in thermally challenging climates (Grémillet et al., 2001). Great cormorants in Greenland were observed to reduce their time spent in water from ~50 min day^{-1} in the summer to ~9 min day^{-1} in the winter (Grémillet et al., 2001). Such a strategy has not been observed in other species within the Phalacrocoracidae family. European shags wintering in Scotland, for example, spend up to 7 h day^{-1} diving in water of around 5–6°C (Daunt et al., in press). Since European shags typically dive to much greater depth and for longer durations than great cormorants, the energetic challenge might be even more pronounced for them. Could it be that the energetic costs associated with foraging in *Phalacrocorax* are overestimated? Grémillet et al. (2005) demonstrated that the plumage of cormorants is only partially wettable (while the outer feather part is wettable, the central part is highly waterproof) and that birds maintain a thin insulating layer of air within their plumage. Hence, insulation during diving might be better, and heat loss lower, than previously expected assuming an entirely wettable plumage. In both bank cormorants (*Phalacrocorax neglectus*) and South-Georgian shags (*Phalacrocorax georgianus*) there is a progressive reduction in abdominal temperature throughout dive bouts (Wilson and Grémillet, 1996; Bevan et al., 1997). This abdominal temperature drop, supposedly reflecting a temperature decline in other tissues as well, was suggested as a mechanism to reduce metabolic rate during diving and increase aerobic dive duration. Given the paucity of data on the energetic costs associated with diving in foot-propelled pursuit divers and the exorbitant costs suggested by previous studies, we felt it was important to investigate the energetic costs associated with diving in another *Phalacrocorax* species, the European shag. Such an investigation is especially important in light of the contrasting foraging strategies pursued by shags and cormorants during winter.

The purpose of this study was: (1) to study the energetic costs associated with diving in European shags and any modifying effects of temperature and food and (2) to assess abdominal temperature changes during diving as a potential mechanism to extend dive duration and save energy.

Materials and methods

Three adult European shags *Phalacrocorax aristotelis* L., one male, two females, with a mean mass of 1.67±0.28 kg (mean ± S.D.) were used in this study. Birds were captured from the Runde colony off the west coast of central Norway in June 2001. They were housed in a sheltered outdoor pen (6 m long × 4 m wide × 2.5 m high) with water tank access, which was part of a larger facility built alongside Hopavågen lagoon, Agdenes community, on the west coast of central Norway. Birds were fed approximately 10–20% of their body mass daily, with a mixed diet consisting of Atlantic herring (*Clupea harengus*) and saithe (*Pollachius virens*), supplemented with vitamins and minerals ('Sea Tabs'; Pacific Research Laboratories, El Cajon, CA, USA). Body mass was determined to the nearest 25 g when birds were post-absorptive and dry, if possible every morning, using a spring balance (Salter Abbey, West Bromwich, UK). Birds maintained a stable body mass throughout most of the study (July–October 2001). However, daily food intake and body mass increased in mid-October, coinciding with a decline in ambient temperature. Bird capture and all experimental procedures were conducted under permission of the Directorate for Nature Management (reference number 2001/77 ARTS/VI/IDA, 446.7), the County Governor of Møre og Romsdal (reference number 1997/09618/432.41/ME) and the Norwegian Animal Research Authority (reference number 7/01).

Training protocol

Within the first week of capture, the shags were introduced to a v-shaped shallow dive trench (17.5 m long × 2 m wide × 1 m deep) that had been dug, lined with thick PVC sheeting and filled with seawater. Two submersible water pumps (ITT Flygt, Oslo, Norway) provided a continuous exchange with seawater from the adjacent lagoon (~200 l min^{-1}). Over the course of 4 weeks, the surface of the trench was progressively covered with transparent PVC sheets until only a small section remained open at one end. Birds that submerged here swam to the opposite end of the trench where a fish was placed, swallowed the fish underwater and returned to the uncovered section. Eventually, the open section was covered by a floating platform with a metal frame in its centre that allowed placement of a Plexiglas dome, serving as a respiration chamber. Starting 2 weeks before data collection, birds were captured every day, weighed and placed inside the dome. Birds dived continuously while the respirometry system was running. Training trials lasted between 10 and 30 min and ended when a bird stopped diving voluntarily for more than 5 min. At the end of a trial, the bird was released from the chamber and returned to its pen.

Respirometry system

Oxygen consumption was measured using an open flow-through respirometry system (Sable Systems, Henderson, NV, USA). To measure the metabolic rate during shallow diving, we used a transparent Plexiglas dome in the shape of a truncated pyramid as the respiration chamber (0.6 m long × 0.6 m wide × 0.4 m high; volume, 50 litres), which was partially immersed and received outside air through small holes on its four sides just above the waterline. Similarly, to measure *RMR* in air we used a 55-litre bucket (0.35 m diameter × 0.65 m height) with an airtight Plexiglas lid where air was drawn in *via* four small side holes near its bottom. Air from the respiration chambers was fed directly into the laboratory, which was set up inside a hut adjacent to the dive trench (Fig. 1). Airflow from the respiration chamber was dried using silica gel before being led into a mass-flowmeter (Sierra Instruments Inc., Monterrey, CA, USA), which

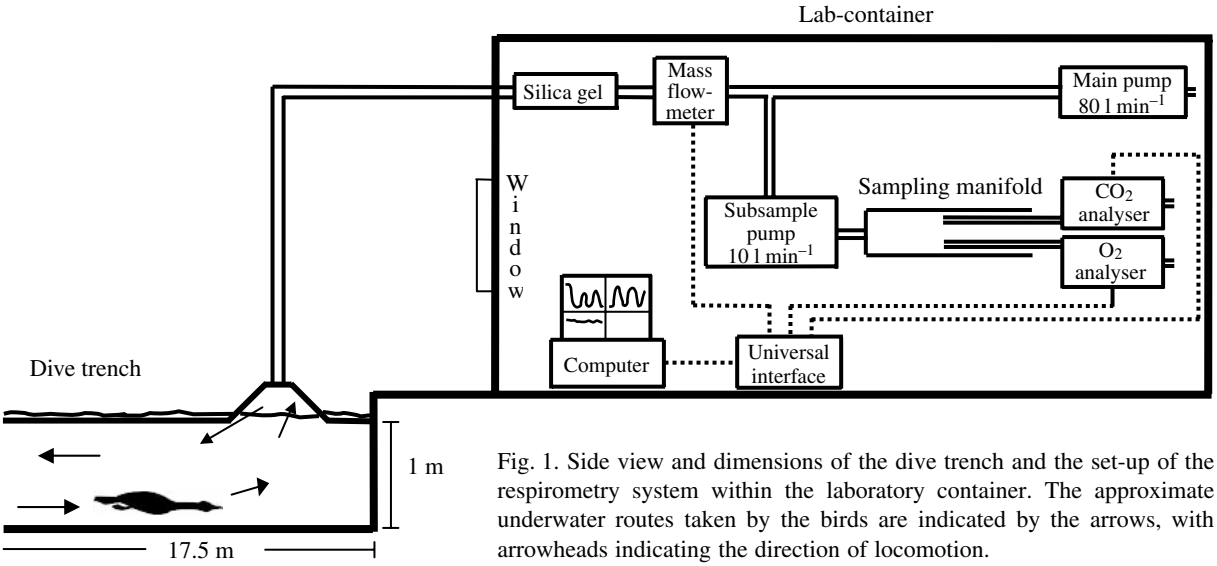

Fig. 1. Side view and dimensions of the dive trench and the set-up of the respirometry system within the laboratory container. The approximate underwater routes taken by the birds are indicated by the arrows, with arrowheads indicating the direction of locomotion.

automatically corrected the measured flow to STPD (273 K and 101.3 kPa). A sub-sample of 10 l min^{-1} was bled into a manifold from which an oxygen (paramagnetic O_2-analyser PA-1B; Sable Systems; resolution, 0.0001%) and CO_2 analyser (Beckman LB2 Medical CO_2-analyser, Schiller Park, IL, USA; resolution, 0.01%) sampled in parallel. All connections between the various components of the respirometry system were made with gas-impermeable Tygon tubing.

Air flow through the respiration chamber was maintained at ~10 l min^{-1} during the resting-in-air trials and at ~80 l min^{-1} during the dive trials (Piston pump; GAST Manufacuring Inc., Benton Harbour, MI, USA). Oxygen concentration inside the respiration chamber was above 20.5%, and CO_2 concentration was below 0.4% during all trials. The gas analysers were calibrated before each trial using pure N_2, 1.03% CO_2 (AGA, Trondheim, Norway) and outside air (set to 20.95% O_2 and 0.03% CO_2). Analyser drift was minimal; nevertheless, any drift was corrected. Before a trial, the entire system was tested for leaks by infusing pure N_2 gas. Time delay between air leaving the respiration chamber and arriving at the gas-analysers was calculated by dividing the total volume of the tubing and drying columns by the corresponding flow rate. The delay was found to be 27.0 s (resting in air) and 16.8 s (diving) for the oxygen analyser and 17.8 s (resting in air) and 7.65 s (diving) for the CO_2 analyser, respectively. These delay times were taken into account when calculating oxygen consumption rates ($\dot{V}_{O_2}$) and CO_2 production rates ($\dot{V}_{CO_2}$) and relating them to diving events. The time constant of the respiration chambers was calculated to be 5.5 min for resting in air and 0.6 min for diving, respectively.

Data from the flowmeter and the gas analysers were fed into a universal interface (16 bits resolution; Sable Systems) and mean values were recorded every 1 s (dive measurements) or 5 s (*BMR* measurements) onto a desktop computer using Datacan (Sable Systems).

Resting metabolism

Basal metabolic rate (*BMR*) was measured during the night (22.00–06.00 h) and day (08.00–18.00 h) while birds were resting, post-absorptive and presumably within their thermo-neutral zone [measurements between 10 and 19°C air temperature; using the equation given by Ellis and Gabrielsen (2002) reveals a lower critical temperature for our birds of ~6°C]. Birds were fasted overnight or for at least 7 h before being placed inside the respiration chamber. After the initial disturbance, birds calmed down quickly and sat quietly in the darkened chamber for the remainder of the trial. A stable $\dot{V}_{O_2}$ was typically reached within the first hour of these 3–5 h-long trials. Air temperature in the respiration chamber was monitored using a digital thermometer (Oregon Scientific, Portland, OR, USA) and usually did not differ from outside air temperature by more than ±2°C. Birds were familiarized with the procedure on at least two occasions before data collection began. *BMR* was determined from at least three trials per bird during September 2001.

Diving metabolism

Diving metabolic rate was measured in all birds during September and October 2001 in water temperatures ranging from 4.9 to 12.6°C. Water temperature was measured after each set of trials 10 cm below the surface. At the beginning of a trial, a bird was captured, weighed and placed inside the respiration chamber, from which it dived continuously. Through the window in the laboratory hut (Fig. 1) it was possible to observe the undisturbed bird. All relevant behaviour of the birds was marked onto the respirometry traces, so that behaviour as well as dive and surface events could be related to the respirometry recordings. In a subset of trials, swim speed was recorded. For this, an observer with a digital stopwatch was placed on a ladder 2 m above ground at the 10 m mark of the dive trench. Swim speed (m s^{-1}) was calculated by dividing the distance swum (10 m)

by the time taken. Only dives in which birds swam in a straight line were included in the analysis. The majority of trials lasted ~20 min (range, 10–50 min), during which birds dived voluntarily and without any interference. A trial was terminated when a bird remained at the surface for more than 10 min. A maximum of two dive trials per bird per day was conducted.

To investigate the effect that feeding might have on diving metabolic rate, birds were diving in both the post-absorptive and absorptive state. For the post-absorptive trials, birds were fasted overnight for at least 15 h. For the absorptive trials, birds were fed various amounts of herring (40–160 g) at various times before a trial (0.5–5 h) and/or ingested herring during a trial.

During some trials, birds would dive very little or not at all but rest at the surface. Stable resting periods from these trials were selected to calculate the metabolic rate during resting on water for both the post-absorptive and the absorptive state. Only resting periods that were separated from any diving activity by at least 5 min were included in the analysis.

Stomach temperature

In parallel with the respirometry measurements, temperature loggers (MiniTemp-xl; length, 70 mm; diameter, 16 mm, mass, 25 g; resolution, 0.03 K; earth&OCEAN Technologies, Kiel, Germany) were employed with all birds to measure stomach temperature during the dive trials. Stomach temperature should reflect abdominal body temperature during post-absorptive dive trials if no food is ingested. Temperature loggers were programmed to record stomach temperature every 5 s and were fed to the birds inside a herring. The loggers were equipped with a spring crown and were not regurgitated by the birds but retrieved when the memory was filled, after about 5 days (Wilson and Kierspel, 1998). After retrieval, the data were downloaded onto a laptop computer, the logger was cleaned, re-programmed and re-fed to the bird.

Data analysis and statistics

Oxygen consumption rates ($\dot{V}_{O_2}$) were calculated using equation 3b in Withers (1977). *BMR* was calculated from the lowest 15-min running average value of $\dot{V}_{O_2}$. Although our respirometry system was sufficiently fast to allow separation of individual dive and surface events, we were interested in obtaining an estimate of the overall energetic costs associated with foraging activity. Hence, we decided to calculate diving metabolic rate (MR_d) as the mean value of $\dot{V}_{O_2}$ during a dive bout from its start until 30 s after the last dive in a bout (i.e. MR_d = oxygen consumption during the entire dive bout divided by the sum of all dive and surface durations within that bout). A dive bout was characterised by continuous diving activity and ended, by definition, when the bird started other activities (e.g. wing-flapping; see Fig. 2) or remained at the surface for longer than 2 min (using a log-survivorship plot as bout-ending criterion; Slater and Lester, 1982). Birds typically started to dive from the moment they were introduced into the respirometry chamber. Because of the intrinsic time constant of our system, however, it took approximately 1 min before our system stabilised at an equilibrium point (see Fig. 2). Dives performed during this time were excluded from analysis. Oxygen consumption rates (ml O_2 min^{-1}) were transformed to kJ using the caloric equivalent corresponding to the respiratory exchange ratio (*RER*) of the birds. The *RER* was calculated by dividing $\dot{V}_{CO_2}$ by $\dot{V}_{O_2}$ and averaged 0.72±0.09 (mean ± S.D.) during resting in air, 0.74±0.07 during post-absorptive diving

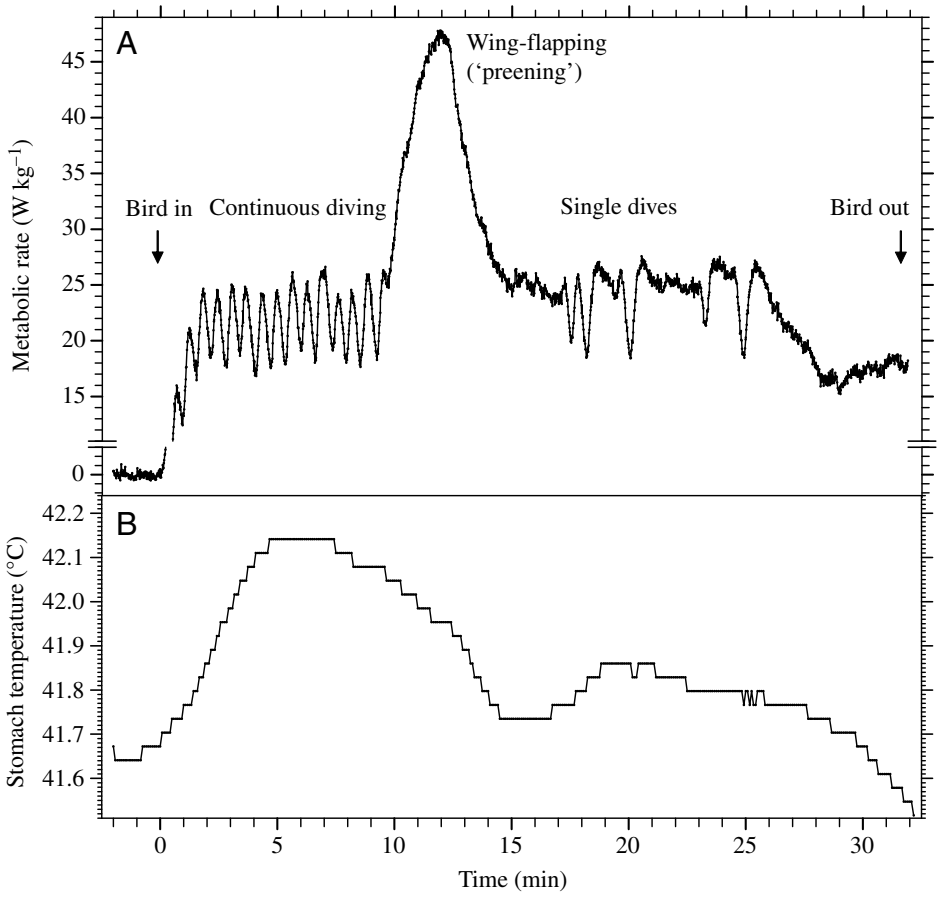

Fig. 2. Respirometry trace (A) and stomach temperature (B) of a European shag during a dive trial (post-absorptive). Arrows indicate when the bird entered and left the respirometry set-up. The trial lasted 32 min in water of 10.1°C. Note, the trace in A does not represent instantaneous metabolic rate but gives an indication of metabolic rate during a dive trial. See Materials and methods for details on how diving metabolic rate was calculated.

and 0.76±0.03 during absorptive diving. Hence, a conversion factor of 19.7 kJ l^{-1} O_2 (Schmidt-Nielsen, 1997) was used to transform these values to Watts (W).

Mass-specific metabolic rate (in W kg^{-1}) is given by: $(19.7\times\dot{V}_{O_2})/(60\times M_b)$, where M_b is body mass in kg and $\dot{V}_{O_2}$ is measured in ml O_2 min^{-1}.

Cost of transport (*COT* in J kg^{-1} m^{-1}) is defined as the amount of energy required to move one unit of body mass (1 kg) over one unit of distance (1 m). We calculated *COT* as the energy expenditure during a dive trial (W kg^{-1}) divided by the mean swim speed (m s^{-1}) during that trial. We included only post-absorptive dive trials in the *COT* analysis, which spanned a temperature range of 5–13°C.

Insight into the insulative properties of birds can be gained by calculating their thermal conductance (*TC*). We calculated *TC* for our shags (post-absorptive trials) when resting in air and water and during diving using the following equation:

$$TC = MR / [(T_b - T_a)\, SA] ,$$

where *TC* is in W m^{-2} $°C^{-1}$, *MR* (metabolic rate) is in W; T_b is the body temperature (mean stomach temperature during a trial) in °C, T_a is the ambient temperature in °C and *SA* is the surface area in m^2, which was estimated using Meeh's formula: $SA=10\times M_b^{0.67}$ (Drent and Stonehouse, 1971), where M_b is in g and *SA* is in cm^2.

Stomach temperatures were analysed using Multitrace (Jensen Software Systems, Laboe, Germany). Resting values during the night and day were established from periods when birds were calm. Temperature recordings were averaged over a period of 6 h during the night (between 23.00 h and 05.00 h) and over periods of at least 2 h during the day (between 08.00 h and 18.00 h). Temperature recordings from the entire period of experimentation were included in the analysis.

Stomach temperatures during the various phases of a dive trial were taken as averages from the first and last minute of a trial ('diving start' and 'diving end', respectively) and as the single highest value during a trial ('diving peak'). Only stomach temperature recordings from birds that had not ingested food for at least 3 h were included in the analysis to exclude periods of decreased stomach temperature after food ingestion.

One-way repeated-measures analysis of variance (ANOVA) with Tukey pairwise multiple comparisons was used for comparison of metabolic rate during different activities and feeding status and for comparing stomach temperatures during various phases. When single comparisons were made, as in comparing *BMR* measured during the day and during the night, Student's paired *t*-test was used. Significance was accepted at $P<0.05$. The relationship between energy expenditure and water temperature that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each bird being assigned a unique index variable (Glantz and Slinker, 1990). All mean values are presented with standard deviation (±1 S.D.).

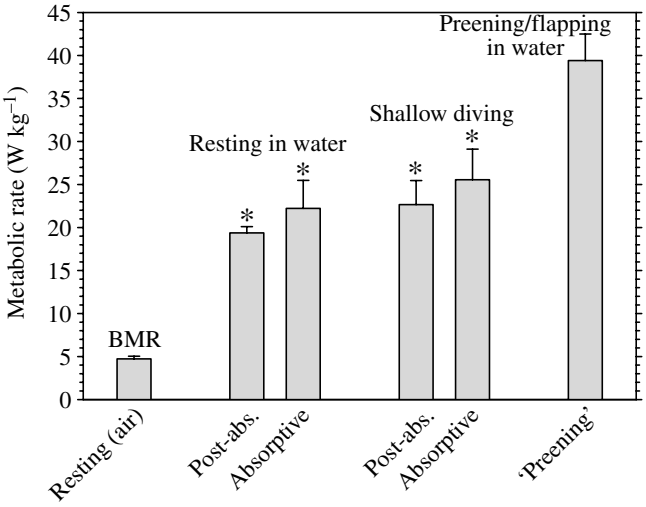

Fig. 3. Metabolic rate of European shags during various activities. Basal metabolic rate (*BMR*) was measured in air temperatures between 10 and 19°C. All measurements in water were made at water temperatures between 5 and 13°C. Values are grand means ± 1 S.D., which were established from individual bird means. $N=3$ birds for all activities except 'preening', where $N=1$ bird. Asterisks indicate a significant difference from *BMR*.

Results

BMR measured at night and during the day was not significantly different ($t=0.71$; $P=0.55$), hence the data were pooled. When resting in air (10–19°C), *BMR* was 4.73±0.31 W kg^{-1} (Fig. 3). Repeated-measures ANOVA comparisons of shag metabolic rate during different activities and feeding status showed that resting in water, diving and feeding significantly elevated metabolic rates above resting rates in air ($F=58.98$, $P<0.001$; Fig. 3). Resting in water significantly elevated metabolic rate (when compared with resting in air) to 19.37±0.73 W kg^{-1} and 22.23±3.25 W kg^{-1} in the post-absorptive and absorptive state, respectively. During diving, metabolic rate increased further to 22.66±2.81 W kg^{-1} in the post-absorptive state and 25.55±3.57 W kg^{-1} in the absorptive state (Fig. 3). Metabolic rate during diving was not significantly different, however, from birds resting at the surface ($t=1.68$, $P=0.23$). Feeding before a trial increased the metabolic rate during diving and when resting in water by an average of 13% and 15%, respectively (Fig. 3). Diving metabolic rate remained elevated for up to 5 h after feeding, which was the maximum period tested. Preening and flapping (wing flapping in preparation for take-off at the end of a dive bout) was the most costly activity, averaging 39.41±3.09 W kg^{-1} in one of the birds displaying this behaviour (Fig. 3).

Water temperature had a significant effect on post-absorptive diving metabolic rate, so that metabolic rate increased with a decrease in water temperature (Fig. 4). The equation relating post-absorptive diving metabolic rate to water temperature was: $MR=28.461-0.671T_w$, where T_w is water temperature in °C and *MR* is measured in W kg^{-1} ($P<0.01$, $t=-3.52$, $r^2=0.69$).

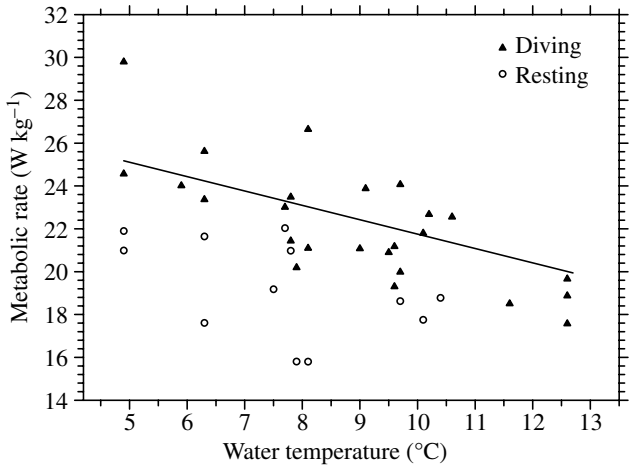

Fig. 4. Metabolic rate of post-absorptive European shags during diving (triangles) and when resting on the water surface (circles) at various water temperatures. There was a significant negative relationship between metabolic rate and water temperature during diving. The regression line shows the average relationship for all shags, which takes into account variability between subjects. It is best described by y=28.461–0.671x (r^2=0.69, N=3 birds, n=25 trials), where y is metabolic rate during diving and x is water temperature. During resting, there was a non-significant trend for metabolic rate to increase with a decrease in water temperature (N=3 birds, n=12 trials).

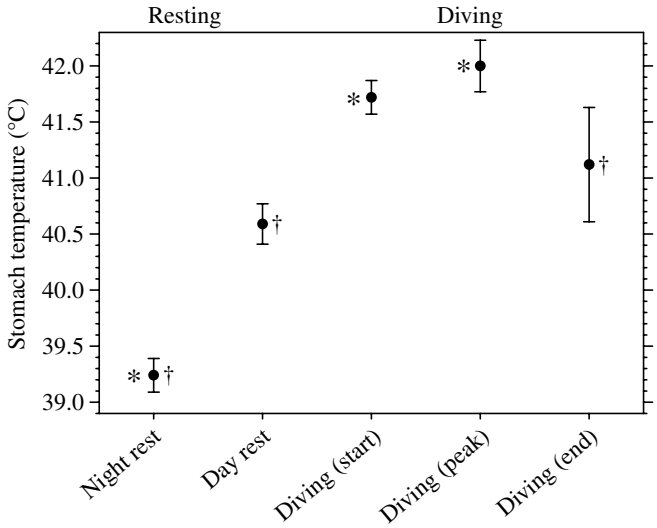

Fig. 5. Stomach temperatures of European shags during rest at night and during the day and during diving. Values are grand means ± 1 S.D., which were established from individual bird means. N=3 birds. *Significantly different from day (rest) value. †Significantly different from diving (peak) value.

However, when diving in the absorptive state, this relationship was not significant (P=0.45, t=–0.76), most likely because of confounding factors. For these dive trials, birds were fed different amounts of food at different times before diving, which could have masked the effect of water temperature on diving metabolic rate. Declining water temperatures also increased the metabolic rate of shags resting on the water surface. Resting in water of 5°C increased the metabolic rate of shags by 17% when compared with resting in 10°C water. This was similar to the 16% increase observed in metabolic rate when water temperatures declined during post-absorptive diving.

Shags swam with a mean speed of 1.1±0.1 m s^{-1} (range, 0.9–1.3 m s^{-1}) and remained submerged for a mean duration of 23.7±2.9 s (max, 57 s). The mean surface interval following a dive was 31.5±6.7 s, and the resulting dive-to-pause ratio was 1.32±0.40. On average, 46% of each dive cycle (dive and subsequent surface interval) was spent underwater.

When plotting *COT* against swim speed, the relationship was best described by an inverse first-order polynomial regression with a minimum *COT* value of 17.8 J kg^{-1} m^{-1} at a swim speed of 1.3 m s^{-1} (r^2=0.48, P=0.018).

Thermal conductance when resting in air of 10–19°C was 2.05±0.16 W m^{-2} °C^{-1} and tripled when floating on water of 5–13°C (6.64±0.28 W m^{-2} °C^{-1}). Diving within the same temperature range increased thermal conductance even further to 7.88±0.5 W m^{-2} °C $^{-1}$, almost four times the value when resting in air. There was no detectable change in *TC* with a decrease in water temperature within the range tested (P=0.62, t=–0.50).

Mean stomach temperature when resting during the day was 40.6±0.2°C, which declined significantly during the night to 39.2±0.1°C (Fig. 5). At the start of a dive trial, temperature was significantly elevated from the daytime resting value and continued to rise during diving. After about 5–10 min of diving, however, a peak was reached after which temperature started to decline (Fig. 2B). Stomach temperature at the end of a dive trial was significantly lower than the peak value reached during diving, but this drop was not significant when compared with the temperature at the start of a dive trial (Fig. 5). The mean temperature increase early in a dive trial was ~0.3°C, while temperature at the end of a trial was, on average, ~0.6°C below the temperature at the start. Stomach temperature changes during a dive trial and the cooling rate (°C min^{-1} in water) were not affected by the water temperature during a trial. Temperature drop and cooling rate were similar during trials in warm and cold water (range, 5–13°C).

Discussion

Diving metabolic rate

Our study shows that the energetic costs associated with shallow diving in European shags are considerably lower than in great cormorants. During post-absorptive diving in water of 5–13°C, the mean energy consumption of shags (22.66±2.81 W kg^{-1}) was ~25% less than in great cormorants diving under similar conditions (31.4 W kg^{-1} – Schmid et al., 1995; 29.1±3.1 W kg^{-1} – Grémillet et al., 2003). Based on our measurement of *BMR* for the shags (4.73±0.31 W kg^{-1}), this would correspond to a diving metabolic rate of 4.8× *BMR*, which is about half of what has been suggested for great cormorants diving in shallow and moderately warm water

(9–12× *BMR*; Schmid et al., 1995; Grémillet et al., 2003). This discrepancy can be partly explained by the very low *RMR* that was measured in great cormorants (3.1 W kg^{-1} for 2.43 kg birds; Schmid et al., 1995), so that diving metabolic rates expressed as multiples of *RMR* become exorbitant. While this value has been used widely in the literature, it is well below the predicted *BMR* of 4.14 W kg^{-1} for a seabird of its mass (Ellis and Gabrielsen, 2002) and the measured value for the Japanese sub-species, *Phalacrocorax carbo hanedae* (4.28 W kg^{-1}; Sato et al., 1988). Using the latter value would result in a diving metabolic rate for great cormorants of between 7.3 and 6.8× *BMR*.

The *BMR* we measured in European shags is almost identical to the predicted *BMR* of 4.60 W kg^{-1}, again using the allometric equation given by Ellis and Gabrielsen (2002), which is based on 77 seabird species. It is slightly lower, however, than the *BMR* value for European shags measured by Bryant and Furness (1995; 5.28±0.22 W kg^{-1}).

The energetic costs of diving in European shags (expressed as multiples of *BMR*) are thus comparable to dive costs of other foot-propelled divers that have been investigated (Table 1). They are, however, considerably higher than dive costs observed in most wing-propelled divers. The energetic costs associated with diving are generally higher in foot-propelled than wing-propelled divers, with diving metabolic rates ranging between 3–5 and 2–4× *BMR*, respectively (Table 1). This general difference might be the consequence of an inherently lower efficiency of foot propulsion, which is mostly drag based, when compared with wing propulsion, which is mostly lift based (Lovvorn and Liggins, 2002). Wing propulsion allows thrust on both upstroke and downstroke, whereas foot propulsion in most species has little or no thrust on the upstroke (but see Johanssen and Norberg, 2003). While some foot-propelled divers (e.g. South Georgian shags; Bevan et al., 1997) achieve dive performances (in terms of dive depth and swim speed) that are comparable with that of wing-propelled divers, Lovvorn and Liggins (2002) suggested that they might do so at great locomotor cost.

Cormorants and shags are both foot-propelled divers, so the propulsive mechanism alone is not likely to explain the observed difference in their diving metabolic costs. However, European shags are considerably smaller in size than great cormorants and their body shape is slimmer and more streamlined when compared with the more bulky great cormorant. Hydrodynamic drag is the most important mechanical cost during steady swimming in birds that dive to depth, where work against buoyancy will be reduced. Lovvorn et al. (2001) showed that the hydrodynamic drag experienced by diving birds strongly depends on body size and shape. Hence, the drag experienced by European shags during diving might be reduced when compared with the great cormorant, in turn lowering energetic costs.

Another important factor to consider is buoyancy. In fact, the high diving costs observed in foot-propelled benthivore ducks (as indicated by Table 1) are mostly caused by the large amount of air trapped within their respiratory system and plumage (Lovvorn and Jones, 1991). Stephenson (1994) found that buoyancy was the dominant factor determining dive costs in lesser scaups diving to the bottom of a 1.5 m-deep tank. Buoyancy accounted for ~75% of the mechanical cost of underwater locomotion in these ducks. In foot-propelled pursuit divers, such as cormorants and shags, overall buoyancy is reduced when compared with diving ducks (Lovvorn and Jones, 1991). While this would tend to decrease diving costs, it should be stressed that cormorants and shags are still highly buoyant, answering to the demands of aerial flight. Double-crested cormorants (*Phalacrocorax auritus*) have a specific buoyancy of 2.7 N kg^{-1} (Lovvorn and Jones, 1991) and ascend passively by means of positive buoyancy from dives to 10 m depth (Enstipp et al., 2001). Hence, work against buoyancy might still contribute heavily to the overall dive costs in cormorants and shags, especially when diving in shallow tanks. In this context, it is interesting to note that cormorants evolved a dynamic buoyancy control mechanism that enables them to counter the destabilizing effects of buoyancy at shallow depth simply by tilting their body and tail (Ribak et al., 2004). While this tilting behaviour would tend to increase drag and, hence, energetic costs, the authors speculated that this might be at least partly offset by the fact that cormorants use a burst-and-glide pattern during diving. When diving in the wild, great cormorants typically descend to shallow depths, where work against buoyancy might still be substantial (mean dive depth, 3–7 m; Grémillet et al., 2001). European shags, on the other hand, dive to depths where costs associated with overcoming buoyancy will be greatly reduced (mean dive depth, 26 m; range, 4–61 m; Wanless et al., 1997), decreasing the overall dive costs in European shags when compared with great cormorants. However, since shags in our study dived within a 1 m-deep trench, this cannot explain the measured difference in diving metabolic rate between both species.

The relatively high diving costs observed in cormorants and shags might also be the result of their poor insulation, increasing thermoregulatory costs. In support of this, Table 1 shows that the metabolic rates of ducks resting on water are similar to their resting rates in air, indicating a good insulation and low thermoregulatory costs. By contrast, metabolic rate in great cormorants and European shags is greatly increased when floating on water (4.5 and 4.1× *BMR*, respectively), indicating greater heat loss and thermoregulatory costs when compared with resting in air. Similarly, Ancel et al. (2000) reported a metabolic rate for Brandt's cormorants of 10.9 W kg^{-1} when resting in warm water (20°C) during the day. This would correspond to 2.5× *BMR* (*BMR* predicted from the allometric equation provided by Ellis and Gabrielsen, 2002). Heat loss will be further increased during diving, when the insulating plumage air layer will be compressed by the increase in hydrostatic pressure and when movement through the water will disturb the boundary layer. De Vries and van Erden (1995) found that the thermal conductance of aquatic bird carcasses increased by a factor of 4.8 during diving when compared with air. In our study, the thermal conductance of European shags increased by a factor of 3.8 during diving. In great cormorants

(using data from Grémillet et al., 2003) thermal conductance was not only higher in absolute terms but it also increased by a greater factor (4.4) during diving, indicating better insulative properties in European shags. We used the heat loss model developed by Grémillet et al. (1998) and our measurements of energy expenditure during diving to estimate the minimal insulating plumage air volume in European shags. The value of 0.38×10^{-3} m^3 at a depth of 1 m corresponds to a 2.71 mm air layer, which is ~60% greater than the calculated value for great cormorants. Hence, a thicker plumage air layer in shags will provide a better insulation, reducing heat loss during diving. This will be especially important for shags during winter, when they spend extended periods foraging in cold water. Heat generated by muscular activity during diving will also help to reduce thermoregulatory costs.

Factors modifying diving metabolic rate

Water temperature had a marked effect on metabolic rate of shags during diving and when resting in water, so that metabolic rate increased when water temperature decreased (Fig. 4). Relatively few studies have investigated the effect that water temperature has on the metabolic rate of unrestrained birds resting in water or diving. In tufted ducks (*Aythya fuligula*), common eiders (*Somateria mollissima*), common murres (*Uria aalge*), thick-billed murres (*Uria lomvia*) and little penguins (*Eudyptula minor*) that rest in water, metabolic rate increased with a decrease in water temperature, which was especially drastic at water temperatures below the point of thermal neutrality (Bevan and Butler, 1992; De Leeuw, 1996; Jenssen et al., 1989; Croll and McLaren, 1993; Stahel and Nicol, 1982). To our knowledge, the effect of water temperature on diving metabolic rate has only been investigated in tufted ducks (Bevan and Butler, 1992; de Leeuw, 1996) and great cormorants (Grémillet et al., 2003). The increase in metabolic rate with a decrease in water temperature observed in our study during diving and when resting in water (16% and 17%, respectively) was similar to what has been found in other aquatic birds. The following comparisons are all based on calculations covering the same temperature range investigated in our study (4.9–12.6°C). Metabolic rate of tufted ducks resting in water and diving increased with a decline in water temperature by 12% and 8.5%, respectively (de Leeuw, 1996). Similarly, in diving great cormorants, metabolic rate increased by 17% when water temperature declined (Grémillet et al., 2003). The greatest increase observed, however, was in common and thick-billed murres when resting in water (28% and 30%, respectively; Croll and McLaren, 1993). It is not intuitively obvious why this temperature effect on metabolic rate should be the strongest in two species that, outside the breeding season, spend their entire time at sea with water temperatures below their lower critical temperature (15°C; Croll and McLaren, 1993). The increase in metabolic rate of shags with declining water temperature was linear throughout the temperature range tested. This suggests that the point of thermal neutrality for European shags in water is above 12.6°C, the highest temperature tested in our study.

The increase in metabolic rate that accompanies the process of digestion, assimilation of food and nutrient interconversion by animals is known as the ‘heat increment of feeding’ (HIF; Brody, 1945). Heating ingested cold food to body temperature also requires energy and will elevate metabolic rate further. Feeding before a trial elevated metabolic rate in shags during diving and when resting in water by an average of 13% and 15% above the post-absorptive rate, respectively (Fig. 3). This is similar to the increase observed in common and thick-billed murres when diving after food ingestion (fig. 1 in Croll and McLaren, 1993). An increased metabolic rate during diving would tend to reduce dive duration, as the available oxygen during a dive would be used up at a faster rate. Birds diving in the wild might therefore structure their foraging bouts accordingly. The increase in metabolic rate that we observed in our shags is lower than the increase observed in thick-billed murres after food ingestion when resting in air (40%; Hawkins et al., 1997) or in sea otters (*Enhydra lutris*) when fed while resting in water (54%; Costa and Kooyman, 1984). The latter authors suggested that otters might use the heat produced from the HIF to substitute for heat that otherwise has to be generated by activity or through shivering and, hence, reduce thermoregulatory costs. This could be an important energy-saving mechanism, especially for aquatic animals where foraging is often interspersed with long resting bouts on the water surface. However, European shags typically do not spend extended periods of rest on the water surface after a foraging bout but rather leave the water to rest on land. During chick rearing, European shags in Scotland spent ~85% of their daily time resting at the colony (Enstipp et al., in press). Cool air temperatures, wet and windy conditions are often prevalent and might require heat production that could be augmented by the HIF. Furthermore, stomach temperature of shags in our study remained elevated throughout dive trials even in 5°C water. If this also holds true for their extended dive bouts during winter (up to 7 h; Daunt et al., in press) the additional heat generated by the HIF could be important in offsetting thermoregulatory costs during these dives. If, on the other hand, European shags, like South Georgian shags, allow body temperature to fall during these long dive bouts, the HIF might be an energetically inexpensive way of replacing heat lost during diving at the end of a foraging bout (Bevan et al., 1997). Heat generated during flight, when shags leave the foraging area, might contribute even stronger to this end.

Stomach temperature

The stomach temperature patterns of diving European shags recorded in our study are similar to patterns observed in wild shags (Grémillet et al., 1998). Stomach temperature of shags in our study remained elevated throughout dive trials lasting up to 50 min in water as cold as 5°C (Figs 2B, 5). This is similar to the situation observed in great cormorants diving under comparable conditions (Schmid et al., 1995; Grémillet et al., 2001). Hence, unlike in South Georgian shags or bank cormorants, there is no evidence that European shags or great cormorants might employ a strategy of regional hypothermia

to potentially lower energetic costs and increase aerobic dive duration (Bevan et al., 1997).

Our study has shown that the energetic costs during shallow diving in European shags are considerably lower than in great cormorants and are comparable with other foot-propelled divers. This difference might be partially explained by lower hydrodynamic costs during diving in the shags, owing to their smaller size and more streamlined body shape. It might also be explained by a better thermal insulation in shags, reducing thermoregulatory costs during diving. Water temperature and feeding status had a strong impact on diving energetics in shags, so that metabolic rate increased with declining water temperatures and remained elevated after food ingestion for up to 5 h. We found no evidence that European shags might employ a strategy of regional hypothermia, since stomach temperature remained elevated throughout dive trials. Shags in this study were diving within a shallow dive trench. Hence, the effects that depth might have on the energetic costs during diving could not be evaluated. The increase in ambient pressure when diving to depth will decrease the amount of air trapped within the plumage and hence thermal insulation. The resulting increase in heat loss might outweigh any energetic advantages that a decreased buoyancy at greater depth might produce, especially if water temperature is low. However, the energetic consequences of diving to depth remain to be investigated.

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