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Energetics of underwater swimming in the great cormorant (*Phalacrocorax carbo sinensis*)

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Abstract Resting metabolic rate (RMR), energy requirements and body core temperature were measured during underwater swimming in great cormorants (*Phalacrocorax carbo sinensis*) at the zoological garden in Neumünster, Germany, using gas respirometry and stomach temperature loggers. We used a 13 m long still water canal equipped with a respiration chamber at each end. Birds swam voluntarily in the canal at a mean speed of 1.51 m s^{-1} . Power input during underwater swimming averaged 31.4 W kg^{-1} . Minimal costs of transport of $19.1 \text{ J kg}^{-1} \text{ m}^{-1}$ were observed at a speed of 1.92 m s^{-1} . Body core temperature was stable in all birds within the first 60 min spent in the canal. After that, body temperature dropped at a rate of $0.14 \text{ }^\circ\text{C min}^{-1}$ until the birds voluntarily left the water. Our data indicate that great cormorants spend 2.7 times more energy than Adélie penguins (*Pygoscelis adeliae*) during underwater swimming. This can be essentially attributed to their poor insulation, their mode of locomotion underwater and differences in streamlining. RMR on land was related to body mass via $\text{VO}_2 = 0.691 \text{ M}^{0.755}$ (where VO_2 is O_2 -consumption in litre h^{-1} and M is body mass in kg). In order to quantify the effects of external devices on energy consumption during underwater swimming, we tested a dummy data logger attached to the back of the cormorants as well as a ring on the leg. The ring had no apparent influence on the swimming energetics of the cormorants. In birds equipped with dummy loggers, swimming speed was not significantly influenced, but both power input and costs of transport increased by a mean of 19% for swimming speeds between 1.4 and 1.8 m s^{-1} .

Introduction

Determination of the swimming costs in great cormorants is of physiological, ecological and economic interest. As opposed to wing propelled penguins, which have been extensively studied with respect to swimming energetics (e.g. Culik et al. 1994a), cormorants are foot propelled divers with a wettable plumage. This wettability entails a reduction of the air layer over the skin and thus a reduction or even a loss of the insulating capability of the plumage (Wilson et al. 1992). On the other hand, the resulting lack of buoyancy is purported to reduce the energetic costs of diving in shallow water (Wilson et al. 1992). The mechanism by which the plumage gets wet has been extensively studied by different authors (Rijke 1968, 1970; Casler 1973; Elowson 1984; Rijke et al. 1989), but no data on the consequences of this adaptation on body core temperature and swimming costs have been reported.

Furthermore, the recent increase of the European population of the great cormorant *Phalacrocorax carbo sinensis* has led to conflicts between human fisheries and nature conservationists concerning a possible influence of these piscivorous birds on commercial fish stocks (Deufel 1987). These incidents have consequently stimulated cormorant research especially with regard to diet and daily food requirements. Determination of the time energy budget (TEB) in the field and the energetic costs of the various activities using gas respirometry allows the calculation of daily energetic requirements with great accuracy (e.g. Culik 1994; Grémillet et al. 1995) and therefore contributes important data for future discussions.

For that purpose, we wanted to determine swimming costs in great cormorants, since swimming is an important part of the daily activity of these birds and because the wettable plumage makes the use of standard allometric relationships invalid. Our aim was also to assess the influence of rings and back-mounted devices

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on swimming costs. Both methods are widely applied in ornithology, and very little data are available (cf. Calvo and Furness 1992) on their deleterious effects on the birds.

Material and methods

All experiments were carried out under licence between August and October 1993 at the zoological garden in Neumünster (Germany). Four captive great cormorants (*Phalacrocorax carbo sinensis*) were weighed on the first day (15 August; mean = 2310 g, SD = 526) and on the last day of the experiments (13 October; mean = 2560 g, SD = 430). The mean body mass gain per day was calculated, and the mass at the day of the experiment estimated from this for further calculations. The birds were fed by hand to become familiar with the investigators.

Swimming energetics

During a period of three weeks, the birds were trained to swim voluntarily through a still-water swim-canal, 13 m long, 0.9 m wide and 0.9 m deep. The canal was placed in a large pool and consisted of a steel frame supporting a black polyethylene sheet. Two wedge-shaped respiration chambers (base area 0.5×0.8 m, max. height 0.7 m, volume 95.5 and 81.4 litre, respectively) made of transparent poly-vinyl-chloride were placed at either end of the canal. The canal was sealed 5 cm below the water surface by transparent poly-vinyl-chloride sheets (0.9×3 m) which covered the entire surface between the two chambers, allowing constant observation of the bird's behaviour from above. For that purpose, an observer stood next to the canal, recording the behaviour and position of the bird on a Husky Hunter (Husky, Coventry, England) field computer, which simultaneously recorded time to the nearest 0.1 s. For determination of cormorant position in the canal, the latter was subdivided into seven sections which were marked with tape. The behavioural data files obtained for each experiment were later analysed using specially designed software to yield duration of resting and swimming as well as swimming distance and speed. The tank was cleaned and filled with fresh water every 3 d. Mean water temperature was 12.6°C ($n = 16$, $\text{SE} = 0.08$).

Each cormorant entered and left the canal by itself when one of the respiration chambers was opened, making handling of the birds unnecessary. The bird remained in the canal for an average of 60 min (± 16 min) and was allowed to exit as soon as it stopped swimming and remained in one respiration chamber for more than 5 min. Surfacing and breathing was only possible in the two respiration chambers, where air was renewed at a rate of $2200 \text{ litre h}^{-1}$. A subsample of the air from each chamber was dried and passed onto one of the two paramagnetic oxygen analysers (Maihak, Hamburg). Data from each analyser were sampled every 2 s by a computer. The whole system was calibrated and checked daily using known volumes of nitrogen bled into one of the respiration chambers. Mean measurement error was 2% ($\text{SE} = 0.02$).

Oxygen consumption was analysed with respect to swimming speed and averaged for 0.2 m s^{-1} speed classes ranging from 1 to 2 m s^{-1} . See Culik et al. (1990, 1994a) and Culik and Wilson (1991b) for more details on the system and calculations. Following Bezzel and Prinzinger (1990) the respiratory coefficient (RQ) was assumed to be 0.8 for birds with a high protein diet such as cormorants (Dunn 1976). Conversion into energy consumption was made assuming a conversion factor of 20.1 kJ l^{-1} oxygen (Calder 1974).

Air and water temperatures as well as atmospheric pressures were measured and recorded every 10 min by a micro-meteorological station (Grant, Cambridge, UK). Temperature in the respiration



Fig. 1 Great cormorant carrying a dummy Diving Event Electronic Processor (DEEP) attached on its back

chambers was equal to ambient air temperature. The humidity in the chambers was assumed to be 100%.

To quantify the influence of external devices on the energetics of diving, we employed dummy Diving Event Electronic Processors (DEEP $11.5 \times 1.7 \times 1.9$ cm, mass 36 g) and standard metal rings (1.5×2 cm diameter). The dummy DEEPs were attached to the back of the birds (Fig. 1) using Tesa-Band tape (Beiersdorf AG, Germany) and cable ties as described by Wanless et al. (1991). The dummy DEEP used was constructed and attached according to recommendations made by Bannasch et al. (1994) so as to minimize hydrodynamic drag. Prior to experiments with the leg ring, birds were ringed in standard fashion.

Stomach temperature

According to Bezzel and Prinzinger (1990) stomach temperature is a good index for body core temperature. In order to measure a possible decrease of body temperature in great cormorants, we recorded the stomach temperature during the experiments in the swim canal. We employed a SICUP (Single Channel Unit Processor, Driesen & Kern, Bad Bramstedt, Germany) which essentially consists of a memory chip, a quartz clock, a temperature sensor (range 0 to 50°C) and a lithium battery. The system fits in a watertight titanium housing (72×12 mm) and records the temperature at the surface of the housing every 16 s. After deployment and recovery of the device, data were transferred to a personal computer via an interface. The SICUP's were voluntarily taken by the birds when hidden in herrings (*Clupea harengus*) at least 1.5 h prior to the experiment. The units were egested as pellets the next morning.

Resting metabolic rate on land

RMR on land was also measured using respirometry. With the exception of the respiration chamber (volume 100 litre) the equipment employed was identical to that used in the swim canal experiments. The birds were held in the chamber for an average of 97 min (min. 60 min, max. 168 min, daytime measurements). RMR was measured under conditions defined by Aschoff and Pohl (1970) and Bennet and Harvey (1987): the birds were post-absorptive (after fasting for at least 24 h) and within their thermoneutral range (Kendeigh et al. 1977). The chamber was entirely covered with dark plastic sheets in order to minimize stress during the measurements. Direct observation was not possible, but the position of the birds was checked after O_2 -consumption reached a minimum for more than 10 min. All birds were then found to be standing quietly.

Results

Performance in the canal

Cormorants started swimming immediately after entering the canal. They swam at speeds between 0.9 and

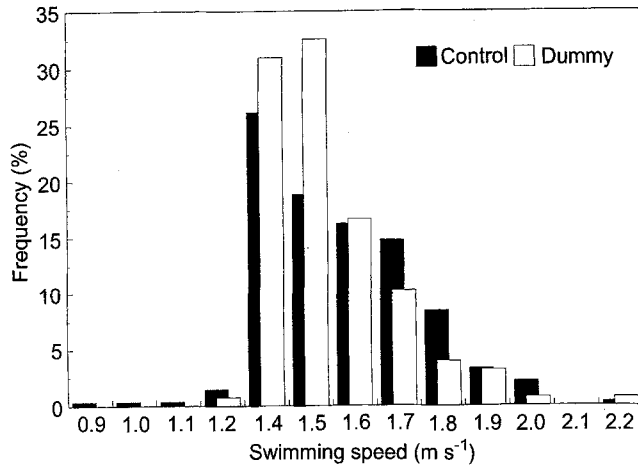


Fig. 2 *Phalacrocorax carbo sinensis*. Distribution of swimming speeds of great cormorants in a 13 m long swim canal as determined via direct observation (*control* without external device; *dummy* with externally attached dummy DEEP)

2.2 m s^{-1} (Fig. 2) with a mean speed of 1.51 m s^{-1} ($n = 348$, $\text{SE} = 0.01$), covering a mean distance of 13 m within 8.6 s ($n = 348$, $\text{SE} = 0.1$). Distances of up to 46 m were reached when birds turned round in the canal without surfacing. The longest recorded dive duration was 41.6 s.

Energy consumption during sub-surface swimming

While resting on the water surface power input (P_r) of the cormorants was 14.1 W kg^{-1} ($n = 16$, $\text{SE} = 0.28$) at a mean water temperature of 12.6°C ($n = 16$, $\text{SE} = 0.08$). Power requirements while swimming (P_s , in W kg^{-1}) were best matched (Fig. 3A) by a cubic function of the type $P_s = 3.6v^3 - 12.2v^2 + 21.5v + P_r$, where v is swimming speed (m s^{-1}) and P_r the energy consumption when resting at the water surface (cf. Culik et al. 1994a).

Transport costs (COT, in $\text{J kg}^{-1} \text{ m}^{-1}$) were obtained using the function $\text{COT} = P_s/v$. The resulting curve fit for great cormorants is shown in Fig. 3B. Minimum transport costs of $19.1 \text{ J kg}^{-1} \text{ m}^{-1}$ occur at a speed of 1.92 m s^{-1} . Due to the small variations in air and water temperatures during these experiments, no relationship between temperature and energy consumption could be found.

Effect of an externally attached device

Cormorants equipped with a dummy DEEP swam slightly, but not significantly (t -test, $p > 0.05$), slower than controls (mean 1.49 vs 1.51 m s^{-1} , median 1.45 vs 1.51 m s^{-1} , $n = 126$ vs 252 , $\text{SE} = 0.01$). However, the mean amount of energy required for swimming at

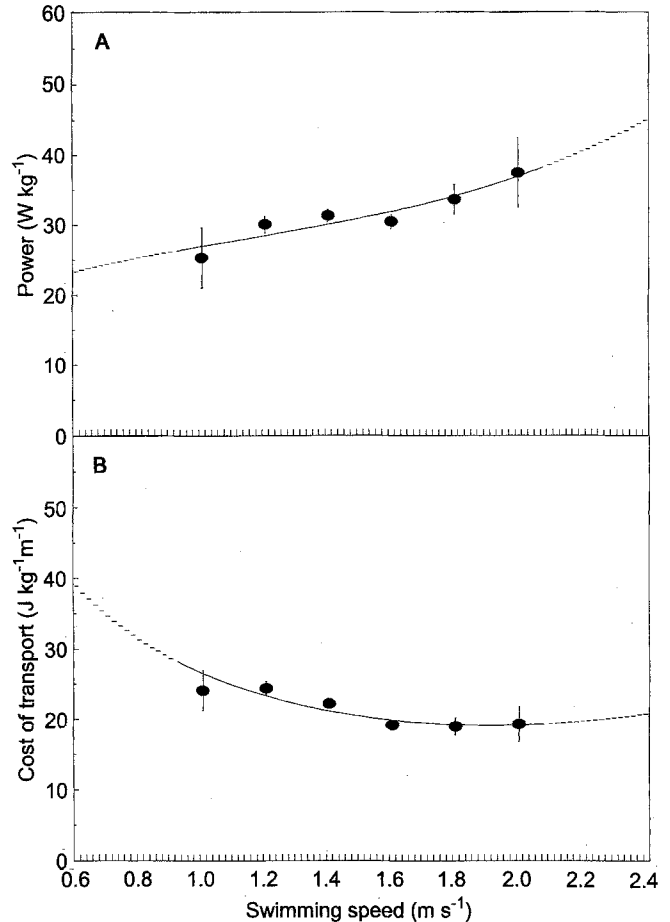


Fig. 3 *Phalacrocorax carbo sinensis*. **A** Power input (W kg^{-1}) in great cormorants ($n = 4$) swimming at will in a 13 m long canal ($r^2 = 0.92$). **B** Transport costs (in $\text{J kg}^{-1} \text{ m}^{-1}$) in great cormorants ($r^2 = 0.93$). Bars show standard error of the means

speeds between 1.4 to 1.8 m s^{-1} was significantly higher (t -test, $p < 0.05$) for cormorants carrying the device (35.1 W kg^{-1} , $n = 126$, $\text{SE} = 0.96$) than without (31.4 W kg^{-1} , $n = 348$, $\text{SE} = 0.58$). COT increased to a mean of $23.7 \text{ J kg}^{-1} \text{ m}^{-1}$ ($n = 126$, $\text{SE} = 0.63$). Mean power and cost of transport increment when swimming with the device at speeds between 1.4 to 1.8 m s^{-1} was 19%. Detailed analysis of the cost of transport ($\text{J kg}^{-1} \text{ m}^{-1}$) as well as power (W kg^{-1}) in the instrumented birds showed an increase by a minimum of 9% at 1.4 m s^{-1} ($n = 73$ treatment vs 145 control), by a maximum of 26% at 1.6 m s^{-1} ($n = 34$ vs 101) and by 23% at 1.8 m s^{-1} ($n = 9$ vs 34) as compared to the unequipped controls.

Effect of a leg ring

Swimming speed (1.52 m s^{-1} , $n = 271$, $\text{SE} = 0.01$), energy requirements (31.5 W kg^{-1} , $n = 271$, $\text{SE} = 0.58$) and COT ($20.9 \text{ J kg}^{-1} \text{ m}^{-1}$, $n = 271$, $\text{SE} = 0.37$) were

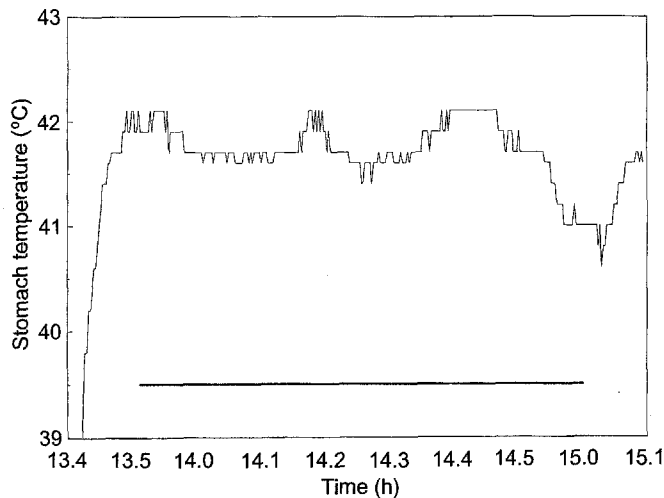


Fig. 4 *Phalacrocorax carbo sinensis*. Example of the drop of stomach temperature ($^{\circ}\text{C}$) of one great cormorant towards the end of an experiment in the swim canal. Temperature measured with a temperature logger fed to the cormorants prior to experiment (first temperature rise). Thick line indicates duration of experiment in the canal

not significantly different between ringed and unringed birds.

Stomach temperature

Mean stomach temperature on land was 41.5°C ($n = 15$, $\text{SE} = 0.18$). A total of eight measurements could be used to estimate changes in stomach temperature while swimming. In six cases the temperature dropped by $0.143^{\circ}\text{C min}^{-1}$ starting approximately 60 min (± 16 min) after the beginning of the experiment (Fig. 4). In the other two cases, no temperature drop could be detected at that time.

Resting metabolic rate

On land, resting great cormorants consumed on average 3.1 W kg^{-1} ($n = 5$, $\text{SE} = 0.15$). Oxygen consumption during rest (VO_2 in litre $\text{O}_2 \text{ h}^{-1}$) was best matched by the allometric relationship $\text{VO}_2 = 0.691 M^{0.755}$ ($n = 5$, $r^2 = 0.93$), where M is body mass in kg.

Discussion

Resting metabolic rate

Our measurements on cormorants were conducted during the active phase and are thus higher than the expected resting metabolic rate (RMR) (Kendeigh et al. 1977). However, although the cormorants were standing as opposed to sitting during the measurements, we

obtained lower values than those of earlier studies for the RMR of a wide variety of birds (e.g. Lasiewski and Dawson 1967). This might be explained by the fact that the birds studied at the zoological garden were particularly tame and thus calmed down quickly once in the respiration chamber.

Swimming energetics

Mean dive time of cormorants in the swim-canal (8.6 s) is relatively low compared to observations made in the wild. Antarctic blue-eyed shags (*Phalacrocorax atriceps*) stayed underwater for 6 to 78 s (Croxford et al. 1991), pelagic cormorants (*P. pelagicus*) dive on average for 34.9 s (Hobson and Sealy 1984), and white-breasted cormorants (*P. carbo lucidus*) for 21.2 s (Wilson and Wilson 1988). Obviously, the distance of 13 m between respiration chambers was too short to reach the dive times observed in nature. However, the birds sometimes did not surface in the respiration chamber, but turned around without breathing, reaching a maximal dive-time of 41.6 s. This shows the ability of captive birds to remain underwater for times similar to those observed in nature.

Junor (1969) gives a mean swimming speed of 1.5 m s^{-1} for *Phalacrocorax carbo*. Unfortunately, there is no data available on the swimming speed of *P. c. sinensis* in the wild, and the discussion about the reliability of the measured speeds in the canal cannot be conclusive. Swimming speeds measured in the canal, however, are expected to be lower than in the wild because the birds had to accelerate and decelerate once every 13 m, something which they would presumably not do in nature. Culik et al. (1994a) report that Adélie penguins swimming in a canal only reached mean speeds of 1.7 m s^{-1} as opposed to 2.2 m s^{-1} in the wild. We therefore expect that *P. c. sinensis* also prefers higher speeds in nature, and presumably swims at speeds which cause the lowest COT, i.e. 1.8 to 2 m s^{-1} .

The cubic function introduced by Culik et al. (1994a) was used to represent the "U"-curve postulated for cost of transport by Schmidt-Nielsen (1983); thus, although at low speeds little energy is used for transport, the distance travelled per second is short, and the result is a comparatively high cost of transport per meter travelled. The lowest part of the "U" indicates the travelling speed at which the relationship of energy input and distance travelled is optimal.

To our knowledge, there are no data in the literature on the swimming energetics of cormorants. Besides several experiments with diving penguins (for example Nagy et al. 1984; Baudinette and Gill 1985; Culik and Wilson 1991a; Culik 1994) the only foot propelled divers which have been investigated in this regard are tufted ducks (*Aythya fuligula*, Woakes and Butler 1983). These experiments, however, were conducted on the water surface. Because of the similarity of the

equipment and the handling during the experiments, our results on diving cormorants can best be compared to the results of Culik et al. (1994a) who worked with three species of penguins in a 21 m long still-water canal in Antarctica.

Energy requirements for underwater locomotion depend primarily on hydrodynamic drag, the work required to overcome buoyancy, and on thermoregulatory costs, especially in cold water. Because cormorants are foot propelled divers whereas penguins use wing propulsion, producing thrust both during the upstroke and the downstroke of the wings (Bannasch 1986; Hui 1988), we expected cormorants to spend more energy while swimming. Although, according to Stephenson et al. (1989) the mechanical efficiency of stroking duck's feet is similar to that of penguin wings, diving ducks probably incur higher drag during the recovery phase when the legs and feet are brought forward again (Lovvorn et al. 1991). This was confirmed by our measurements: great cormorants swam with minimal COT of $19.1 \text{ J kg}^{-1} \text{ m}^{-1}$ at a speed of 1.92 m s^{-1} , whereas e.g. Adélie penguins (*Pygoscelis adeliae*) only required $7.1 \text{ J kg}^{-1} \text{ m}^{-1}$ at their preferred speed of 2.2 m s^{-1} (Culik et al. 1994a). Table 1 shows that Adélie penguins and great cormorants have similar RMR. Whereas the metabolism of Adélie penguins swimming under water is only 4.2 times higher than during rest on land, swimming cormorants spend almost 12 times more energy as compared to resting.

Culik et al. (1994a) presented an equation for the energetic cost of sub-surface swimming in homeotherms. According to their relationship ($\text{COT} = 7.01 \text{ M}^{-0.205}$), minimum COT of the cormorants used in the present study (mean mass 2.43 kg) should have been around $5.8 \text{ J kg}^{-1} \text{ m}^{-1}$, which is only 30% of the value actually measured here. COT in surface-swimming homeotherms, however, is related to body mass by $\text{COT} = 23.8 \text{ M}^{-0.15}$ (Williams 1989). For the birds used in the present study, this would entail transportation costs of $20.9 \text{ J kg}^{-1} \text{ m}^{-1}$, which corresponds very well to our results. It seems from this comparison, that cormorants, as opposed to other species (e.g. penguins), do not derive an energetic advantage from swimming fully submerged.

According to Stephenson et al. (1989) and Butler and Woakes (1984), the buoyancy of a body is the main reason for the high cost of transport during underwater

swimming. Body upthrust is mainly caused by air trapped in the feathers. However, the plumage of cormorants is logged with water during submergence, leading to a reduction in upthrust as opposed to other avian species. Cormorants are almost neutrally buoyant (Wilson et al. 1992). This enables them to hunt at shallow depths, which is what they preferably do (Van Dobben 1952). Wilson et al. (1992) showed that penguins are actually slightly more buoyant than cormorants. Consequently, the differences in COT between penguins and cormorants cannot be explained by differences in upthrust.

The last factor leading to an elevated energy consumption in the water is thermoregulation. Heat conduction in water is 25 times higher than in air. Heat loss must be compensated by heat production and so entails an increased metabolic rate. The wettability of Phalacrocoracidae feathers leads to a loss of metabolic heat during submergence. Great cormorants resting on the water surface spent more energy than penguins: Adélie penguins spent 8.4 W kg^{-1} in water at 4°C (Culik and Wilson 1991a), whereas great cormorants spent 14.1 W kg^{-1} in water at 12.6°C (Table 1). It seems that the reduction in buoyancy achieved by wettable feathers does not compensate for the concomitant increase of metabolism due to thermoregulation.

Core temperature

Penguin plumage is almost water-proof, and most of the insulating air layer over the skin will not be lost even during submergence (Whittow 1986). Loss of this insulation entails an elevation of metabolic rate. Culik et al. (1991) measured oxygen consumption of oiled penguins in a swim canal. The water-proofing quality of the feathers was destroyed, causing loss of buoyancy and insulation. Feathers were completely wet, and the birds shivered on the water surface. The oiled birds tried to leave the water and showed erratic swimming behaviour. Metabolic rate while swimming was 50% higher, and COT was 73% higher than normal. This was also attributed to increased body drag due to the disruption of the oiled plumage.

Using SICUPs in free-living bank cormorants (*Phalacrocorax neglectus*), Wilson and Grémillet (1995) observed a drop in core temperature ($0.12^\circ\text{C min}^{-1}$) 9 min after the birds entered the water. This could not be explained by the uptake of cold food (cf. Grémillet and Plös 1994). In order to elucidate this aspect, we measured stomach temperature in great cormorants in the canal. The temperature loggers actually measured core temperature, which was confirmed by comparing the stomach temperature of our cormorants (41.5°C on land) with the mean core temperature of 41.2°C measured by Whittow (1986). The data obtained from the SICUPs employed showed the tendency of stomach temperature, and thus body core temperature, to fall

Table 1 *Pygoscelis adeliae* and *Phalacrocorax carbo sinensis*. Comparison of resting metabolic rate (RMR), resting on the water surface (Pr) and energy consumption during underwater swimming (Ps) in W kg^{-1} in Adélie penguins and great cormorants

	<i>Pygoscelis adeliae</i>	<i>Phalacrocorax carbo sinensis</i>
RMR	3.8	3.1
Pr	8.4	14.1
Ps	15.6	36.7

when cormorants were in contact with water long enough. Ca. 60 min after the beginning of an experiment in the swim canal, core temperature started to drop.

Although the effect was the same as in bank cormorants, it was observed much later. This may be explained by the meteorological conditions prevailing in the habitat of both species. In South Africa, where bank cormorants were foraging, irradiation was high enough to elevate body temperature rapidly after the birds returned on land. Presumably, bank cormorants could allow their body temperature to drop while in the water, thus saving energy. Great cormorants, on the other hand, might have to regulate their core temperature by increasing their metabolism, since solar irradiation is insufficient to warm them up quickly after a dive sequence. During the experiments in the swim canal, the temperature drop started shortly before the cormorants showed their will to leave the water.

To conclude, we attribute the elevated energy consumption of underwater swimming in cormorants as compared to pygoscelid penguins to the mode of propulsion and the differences in thermoregulation. The absolute importance of each of these factors could not be assessed.

Influence of external devices

External data-recording devices attached to marine animals are used to obtain information e.g. about swimming speed, diving depth and duration of foraging trips at sea and, in the case of rings, population dynamics and distribution. But before employing such devices their effect on the study animal should be evaluated, and their shape, position and attachment optimized. This is also required for the correct interpretation and even correction of the data obtained with the device.

The parameters measured in the swim canal were not affected by the birds carrying leg rings. However, birds equipped with dummy DEEPs had to invest significantly more energy to reach the same swimming speeds as controls, which was also reflected by a higher COT. Culik and Wilson (1991b) showed that Adélie penguins equipped with a dummy DEEP spent more energy than controls and later (Culik et al. 1994b) that streamlined devices caused less drag and energy increment than comparatively smaller, but not streamlined instruments. The effect of the streamlined device on the penguins, however, was still measurable, albeit low (6% mean power increment). This also confirmed the hypothesis of Wilson et al. (1986) that the weight of an external device is only of little importance, because it will be partially buoyed by water displacement.

The data obtained here show that the effects of instrumentation on cormorants are considerable and cannot be ignored. Because any disturbance of the streamlining of an animal's body will cause an increase

in energy consumption during swimming (Culik and Wilson 1991b; Culik et al. 1994b), we chose a dummy DEEP which was designed to match the hydrodynamic properties of a cormorant's body and followed the suggestions of Bannasch et al. (1994). The high additional costs incurred during underwater swimming with the device may stem from the fact that the device (a) changed the location of the centre of gravity of the bird, (b) created rudder effects, which had to be compensated by energetically costly steering manoeuvres on the part of the bird or (c) was simply too large for a bird the size of a cormorant. Because, in the wild, an increase in energetic costs will lead to a higher food intake and thus to an extension of the foraging trips, this may extend the intervals between feeding of the chicks and may cause a reduction of breeding success. Instrument shape and site of attachment will have to be more thoroughly investigated in order to guarantee little disturbance and thus to enable acquisition of meaningful data from free-living cormorants.

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