

ENERGETICS OF SURFACE SWIMMING IN BRANDT'S CORMORANTS (*PHALACROCORAX PENICILLATUS* BRANDT)

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Summary

The energy requirements of Brandt's cormorants (*Phalacrocorax penicillatus*) during surface swimming were measured in birds swimming under a metabolic chamber in a water flume. From the oxygen consumption recordings, we extrapolated the metabolic rate and cost of transport at water speeds ranging from 0 to 1.3 m s⁻¹. In still water, the birds' mean mass-specific rate of oxygen consumption (\dot{V}_{O_2}) while floating at the surface was 20.2 ml O₂ min⁻¹ kg⁻¹, 2.1 times the predicted resting metabolic rate. During steady-state voluntary swimming against a flow, their \dot{V}_{O_2} increased with water speed, reaching 74 ml O₂ min⁻¹ kg⁻¹ at 1.3 m s⁻¹, which corresponded to an increase in metabolic rate from 11 to 25 W kg⁻¹. The cost of transport

decreased with swimming velocity, approaching a minimum of 19 J kg⁻¹ m⁻¹ for a swimming speed of 1.3 m s⁻¹. Surface swimming in the cormorant costs approximately 18% less than sub-surface swimming. This confirms similar findings in tufted ducks (*Aythya fuligula*) and supports the hypothesis that increased energy requirements are necessary in these birds during diving to overcome buoyancy and heat loss during submergence.

Key words: cormorant, *Phalacrocorax penicillatus*, cost of transport, metabolic rate, respirometry, surface swimming.

Introduction

Brandt's cormorants (*Phalacrocorax penicillatus* Brandt) are medium-sized aquatic birds that share their Pacific Coast range with the double-crested (*Phalacrocorax auritus*) and pelagic (*Phalacrocorax pelagicus*) cormorants. At sea, they are often seen floating or swimming at the water's surface between dives. In tufted ducks *Aythya fuligula*, sub-surface swimming is energetically more expensive than surface swimming (Woakes and Butler, 1983). Underwater swimming is also energetically costly for cormorants (Schmid et al., 1995). Sub-surface swimming has been hypothesised to be more expensive energetically in these birds for two reasons. First, although they appear to swim effortlessly at the water surface, they must paddle with their feet to overcome buoyancy and stay submerged (Casler, 1973, Stephenson et al., 1989). Second, although their water-absorbing body plumage (Rijke, 1968; Stephenson et al., 1989) helps to reduce buoyancy and facilitate underwater prey capture, it decreases thermal insulation during submersion. The energetic costs of underwater swimming in cormorants have been studied in detail (Schmid et al., 1995); however, their energy requirements while at rest on water or while swimming on the surface at different speeds have not been investigated. The purpose of the present study was to determine the metabolic cost of surface swimming in cormorants. This allowed us to

compare the energetics of surface activity with that previously measured for underwater activity, and to confirm the previous findings in tufted ducks.

Materials and methods

Birds

Three adult Brandt's cormorants (*Phalacrocorax penicillatus* Brandt) were captured in San Diego Bay in 1994 and housed in individual cages at Scripps Institution of Oceanography (University of California at San Diego, USA). The birds were hand-fed during daylight on a diet of thawed herring (*Clupea harengus*) and smelt (*Salmo eperlanus*) supplemented with vitamins. All birds maintained constant body mass (2.0±0.3 kg, mean ± s.d.) for the duration of their captivity and were released in apparently good health. The respiratory experiments reported here were conducted over a 3 month period. The experimental design was similar to that of Davis et al. (1985); details are provided below.

Water flume

The swimming metabolic rate of cormorants was measured in a flow channel located in the UCSD Hydraulics Laboratory. This channel, 1 m×1 m×16 m, was equipped with a

respirometry dome in the test section placed at the centre of the channel. Closed-loop variable water flows of 0–1.3 m s⁻¹ were generated by two propeller pumps. Water velocity was measured with an electromagnetic flow sensor positioned 30 cm above the floor of the flume. Vertical profiles of water velocity through the test section showed that variation was less than 0.1 m s⁻¹ between the surface and the bottom for water speeds ranging from 0.4 to 1.3 m s⁻¹.

Respiration

The birds swam in a test section covered with a metabolic hood consisting of an oblong Plexiglas dome (1.1 m long, 0.6 m wide and 0.3 m high) mounted in a wooden frame and suspended 10 cm below the surface of the water. Respiration of the bird was restricted to this dome, the dimensions of which gave the minimum chamber volume without interfering with the bird's swimming. The metabolic chamber was connected to an open-flow respirometry system. The system consisted of a modified vacuum cleaner blowing air at 60 l min⁻¹ into a tube connected to the front of the metabolic chamber. Air was sampled by a pump from the rear of the chamber for gas analysis.

Metabolic determinations

The air sample from the outflow from the metabolic dome was pumped through a flowmeter, dried through a Drierite column and scrubbed of carbon dioxide with Baralyme before entering a paramagnetic O₂ analyser (S-3A O₂ analyser; Applied Electrochemistry Inc., Sunnyvale, CA, USA). The analogue output of the O₂ analyser was connected to an on-line computer with an analogue-to-digital interface board. The data were analysed every 1 s using specially designed software that averaged percentage O₂ over 10 s intervals.

Before each swimming session, the entire respirometry system was tested for leaks by infusing pure N₂ gas. The system was then calibrated with ambient air (20.94 % O₂) and gas mixtures of known N₂ content. The theoretical and measured fraction of O₂ in the expired gas line agreed to within 0.01 % at all water velocities tested. The 95 % response time of the respirometry system was 2–3 min. There was no drift in the O₂ analyser for the duration of any of the sampled runs.

Atmospheric pressure and temperature were recorded before and after each experimental session to convert gas measurements to standard temperature and pressure of dry air (STPD).

Swimming runs

Before the respiratory experiments were conducted, the birds had been trained to swim at variable water speeds in the respiratory dome. Four or five practice sessions were required to accustom the birds to the apparatus.

Birds were fasted overnight before swimming sessions in the flume. After being weighed, a cormorant was introduced to the respiratory chamber with the water still. The air flow rate and O₂ analyser zero setting were checked, together with

air and water temperatures. During the first minutes, the birds were sometimes very excited, pecking at the dome of the respiration chamber. Thus, we allowed an acclimation period of 10–15 min before starting a swim. During this time, the birds became quiet. A random schedule of swimming speeds was followed which lasted no more than 60 min. The birds swam for 10–15 min at a given speed. After each experiment, the cormorant was removed from the chamber and the air flow rate and O₂ analyser zero setting were rechecked. Seawater temperature in the flow channel was 19–21 °C for all studies.

Swimming metabolic rate was measured during the day as birds swam against the current in the water channel. Measurements of \dot{V}_{O_2} at rest were taken before, after and between runs, while the birds floated on still water. Resting measurements were also conducted at night; birds at night were fasted for the same length of time as those during the day.

Calculations

A cormorant was considered to be in a steady state if its rate of O₂ consumption varied by less than 5 % over a period of at least 5 min for each swimming speed. Only these stable and reproducible values are reported. \dot{V}_{O_2} was calculated using the equations of Depocas and Hart (1957):

$$\dot{V}_{O_2} = \frac{F[0.2094 - (Y/100)]1000}{1 - (Y/100)}, \quad (1)$$

where F is the air flow corrected to STPD, 0.2094 is the fraction of O₂ in dry, ambient air and Y is the measured percentage of O₂.

$$F = \frac{f(273/K)[P_b - (P_v R/100)]}{760}, \quad (2)$$

where f is the measured air flow (l min⁻¹), K is the measured temperature of air (K), P_b is the measured barometric pressure (mmHg; 1 mmHg=0.1333 kPa), P_v is vapour pressure (mmHg) and R is relative humidity (assumed to be 100 % within the respiration chamber).

Rates of O₂ consumption were transformed to kJ using the caloric equivalent corresponding to the respiratory quotient (RQ) of the birds. This RQ was assumed to be 0.7, so all oxygen recordings were converted to kJ using a factor of 20.1 kJ l⁻¹ O₂ (Schmidt-Nielsen, 1983). These values were then transformed to W.

Thus, metabolic rate (MR, in W kg⁻¹) is given by:

$$MR = 20.1 \dot{V}_{O_2} / 60 M_b, \quad (3)$$

where M_b is body mass (kg).

As defined by Schmidt-Nielsen (1972), the cost of transport (CoT; J kg⁻¹ m⁻¹) is the amount of energy required to move one unit of body mass (1 kg) over one unit of distance (1 m). Thus, we have:

$$CoT = MR/v, \quad (4)$$

where v is the swimming speed (m s⁻¹).

Values are presented as means ± standard deviation.

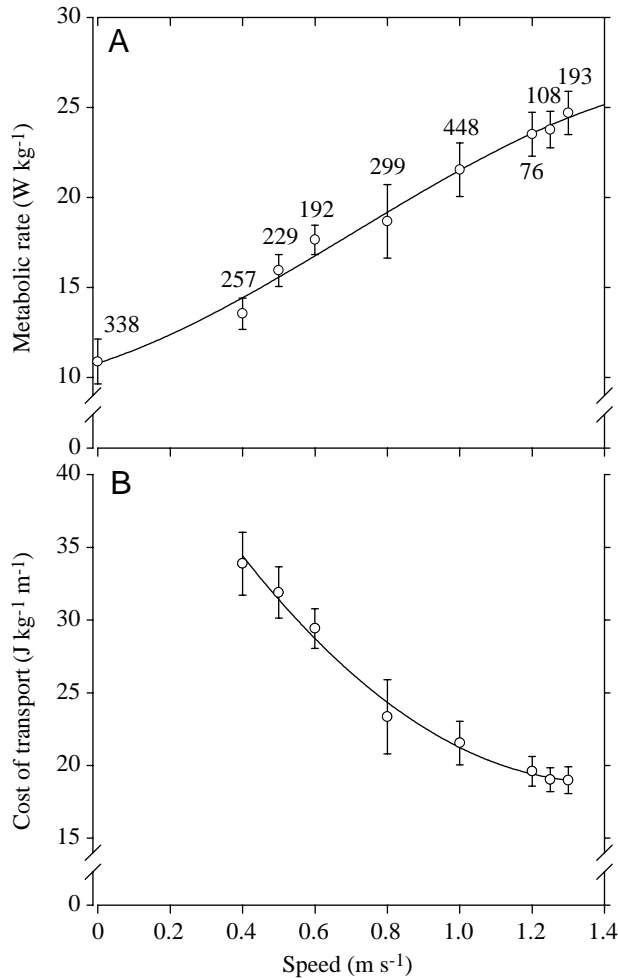


Fig. 1. Metabolic rate (A) and cost of transport (B) plotted as a function of swimming speed for three cormorants. Values are means ± 1 S.D. The number of swimming sessions at each speed is shown. Values at zero swimming velocity are daytime values for cormorants resting on still water. The solid line is the polynomial relationship through the data points (see text).

Results

The birds swam consistently at the surface for water velocities up to 1.3 m s^{-1} , although at speeds higher than 1.0 m s^{-1} they tended to dive. At speeds higher than 1.3 m s^{-1} , waves formed in the flume. Only data from recordings obtained during surface swimming were analysed. For this reason, we obtained only 377 reliable data points (18%) in the range $1.2\text{--}1.3 \text{ m s}^{-1}$, whereas 1763 were obtained for lower water speeds (Fig. 1A). Mean values were calculated after pooling the data for the three birds into speed categories.

Rates of oxygen consumption

During the day, we obtained 2140 usable readings of \dot{V}_{O_2} compared with the 6246 readings obtained at night. All the night values were resting values.

The mean resting \dot{V}_{O_2} of cormorants sitting still on the surface of the water beneath the respiratory chamber during

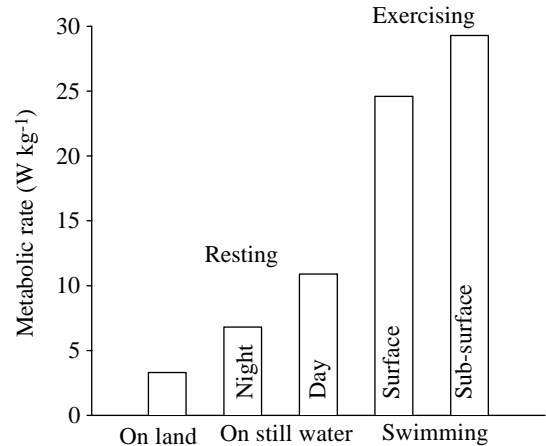


Fig. 2. The metabolic rate of Brandt's cormorants under different situations. From left to right: resting on land (calculated from the equation given by Schmid et al., 1995), resting on still water at 20°C during the night (present study), resting on still water at 20°C during the day (present study), for a bird swimming at the surface with the minimal cost of transport (present study) and for a bird swimming under water (calculated from the equation given by Schmid et al., 1995).

the day was $32.5 \pm 3.7 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($N=338$). Mean \dot{V}_{O_2} was significantly ($P < 0.001$) lower at night ($20.2 \pm 3.6 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, $N=6246$). The \dot{V}_{O_2} of the cormorants increased with flume speed. At the maximum speeds allowed by our apparatus, their \dot{V}_{O_2} was $74 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, approximately 2.3 times the daytime resting level and approximately 3.6 times the night-time resting level.

Metabolic rate and cost of transport

The mean energy expenditure of the three cormorants increased from 10.9 W kg^{-1} while resting during the day to 24.7 W kg^{-1} while swimming at 1.3 m s^{-1} , a 2.25-fold increase (Fig. 2).

During steady-state surface swimming, the cormorant's metabolic rate (MR) increased with water speed and was modelled for the different swimming velocities (v , m s^{-1}) using a third-degree polynomial fit (Culik et al., 1994): $\text{MR} = 10.8 + 6.5v + 8.1v^2 - 3.8v^3$ ($r^2 = 0.99$, $N = 9$, $P < 0.001$). The resulting curve is shown in Fig. 1A.

We obtained the cost of transport (CoT, Fig. 1B) by dividing MR by water speed and obtained the following equation: $\text{CoT} = 49.6 - 44.5v + 16.1v^2$ ($r^2 = 0.99$, $N = 8$, $P < 0.001$).

Discussion

Resting metabolic rate

The metabolic rate of cormorants at rest in water at night was two-thirds of that measured during the day (Fig. 2). We attribute this to the 'calmer' appearance of the birds at night, which may have been due to fewer visual stimuli in the glass-walled flume during the night. Indeed, the birds rarely rested

on still water during the day, so we obtained far fewer daytime data points. Therefore, the night values were considered to be more representative of the resting metabolic rate in water.

Using the allometric relationship established by Schmid et al. (1995), we estimate the metabolic rate of the Brandt's cormorants to be 3.3 W kg^{-1} while resting on land within their thermoneutral zone, a value close to that of 3.1 W kg^{-1} found by those authors in great cormorants (*Phalacrocorax carbo sinensis*). This predicted resting value on land is half the value of 6.8 W kg^{-1} measured when the bird was resting quietly on still water at night (Fig. 2). Similarly, the \dot{V}_{O_2} of mallard ducks *Anas platyrhynchos* resting in air was only 73% of the value during resting on water (Prange and Schmidt-Nielsen, 1970). Woakes and Butler (1983) attributed this difference (air–water) to heat loss to the water. The higher cost in the cormorant than in the mallard duck may be the result of its lower buoyancy (the cormorant floats lower in the water) and also of the wettability and decreased insulation of its plumage. This higher cost in the cormorant is similar to that of the Adélie penguin *Pygoscelis adeliae*, which also floats low in the water (Culik and Wilson, 1991). These observations raise the issue of aquatic thermoneutral zones for these birds. We are unaware of such determinations in these species. However, the water temperatures in our study are typical of those that these cormorants would encounter at sea.

Swimming metabolic rate

Metabolic rate during surface swimming has been observed to increase curvilinearly with speed for mallard and tufted ducks *Aythya fuligula* (Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983), for semi-aquatic mammals (e.g. mink *Mustela vison*; Williams, 1983) and for marine mammals (e.g. seals and sea lions; Williams et al., 1991). In the ducks, \dot{V}_{O_2} at low swimming speeds ($0.2\text{--}0.4 \text{ m s}^{-1}$) was near the resting value, and it increased linearly at higher speeds. This resulted in an overall curvilinear response. In our study of Brandt's cormorants, swimming \dot{V}_{O_2} increased curvilinearly ($r^2=0.991$) with speed from 0 to 1.3 m s^{-1} . Although linear regression analysis of the cormorant data resulted in a high r^2 value (0.982), we suspect that the overall response in the cormorant would have been even more curvilinear had we been able to obtain data at slower swimming speeds ($<0.4 \text{ m s}^{-1}$).

Maximum cruising speed is limited by the effects of waves created by the body. For example, the maximum sustainable speed of mallard ducks coincided with their predicted hull speeds (Prange and Schmidt-Nielsen, 1970). Hull speed is the velocity at which the bow wave constructively interferes with the stern wave of an object in the water. At that point, the hull of the object is entrapped in the trough between the bow and stern waves. Drag increases asymptotically as hull speed is approached (Prange and Schmidt-Nielsen, 1970). Hull speed is dependent on the waterline length of the body. Like the black duck *Anas rubripes* (Baudinette and Gill, 1985), Brandt's cormorants were reluctant to swim on the surface at speeds higher than 1.0 m s^{-1} ; at this speed, they attempted to dive. The cormorants used in the present study had a water-line length

of 0.55 m (Wallace and Wallace, 1998). From this length, a hull speed of 0.9 m s^{-1} can be calculated (Prange and Schmidt-Nielsen, 1970). The agreement between this hull speed and the observed maximum sustained swimming speed of the cormorants used in this study (1.0 m s^{-1}) implies that the swimming speed of the cormorants is subject to the constraints found in other studies (Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983; Baudinette and Gill, 1985); \dot{V}_{O_2} increased approximately two- to threefold above resting levels as the theoretical hull speed was approached. In all studies, birds rarely swam at the surface at higher speeds. Furthermore, cormorants are not surface-swimming specialists: they prefer to stay quietly at the water surface instead of actively swimming. In contrast, they are able to swim under water at speeds as high as 1.5 m s^{-1} (Schmid et al., 1995) to pursue and catch their prey, even though they tended to dive when surface water velocity exceeds 1 m s^{-1} .

Cost of transport

The minimum cost of transport is a useful way to compare animals of different size because it is independent of speed and is constant for each animal (see Schmidt-Nielsen, 1972). Animals that swim and fly characteristically show a U-shaped relationship between speed and cost of transport, with a minimum cost of transport at intermediate speeds (Prange and Schmidt-Nielsen, 1970). When the cost of transport for the cormorants was plotted against swimming speed (Fig. 1B), a minimum value of $18.9 \text{ J kg}^{-1} \text{ m}^{-1}$ (1.3 m s^{-1}) was obtained. Although we were unable to obtain measurements at higher swimming speeds, in the light of the hull speed analysis above, we suspect that our minimum value represents the bottom of the U-shaped cost of transport/speed relationship for surface-swimming cormorants.

Surface versus sub-surface swimming

Cormorants consume 18% less energy when they are swimming at the water's surface (Fig. 2) than when they are swimming below the surface (data from Schmid et al., 1995). This finding is similar to that for tufted ducks (Woakes and Butler, 1983). The lower \dot{V}_{O_2} during surface versus sub-surface swimming may be secondary to several factors, including drag, buoyancy and/or heat loss. Although the drag of a towed duck carcass torso (no legs) is lower at the surface than when submerged (Stephenson et al., 1989), differences in drag are an unlikely explanation for the \dot{V}_{O_2} difference because of the modes of surface and sub-surface swimming in cormorants, which use alternate strokes of their feet during surface swimming, but stroke their feet in unison during diving. According to several sources, alternate stroking is uneconomical because of greater drag (Prange and Schmidt-Nielsen, 1970; Stephenson et al., 1989).

Buoyancy probably contributes significantly to the difference between the cost of surface and sub-surface swimming. Stephenson et al. (1989) have calculated that 95% of the work performed during diving of the lesser scaup *Aythya affinis* is used to overcome buoyancy. Similarly, McPhail and

Jones (1998) reported that a 41 % reduction in buoyancy of the lesser scaup resulted in a 61 % decrease in the calculated mechanical power output during the feeding phase of a dive.

Heat loss may also be a significant factor. First, Schmid et al. (1995) obtained their data at a water temperature 7 °C lower than ours, which may have contributed to the difference in metabolic rates. However, it is noteworthy that the $\dot{V}O_2$ of a tufted duck during a 13.5 s dive is 21 % higher than that measured at the same water temperature for a tufted duck swimming at the surface at the maximum sustainable speed (Woakes and Butler, 1983). Another thermal mechanism that may account for differences between surface and sub-surface metabolic rates is wetting of the plumage. While swimming at the surface, only the ventral plumage gets wet, whereas in diving cormorants the body is completely in contact with the water, and the maintenance costs of homeothermy should be greater. Because the heat capacity of water is 25 times greater than that of air, water contact may increase the thermal conductance of aquatic birds by a factor of 2.2 during swimming and by a factor of 4.8 during diving (De Vries and Van Eerden, 1995).

In summary, buoyancy and greater heat loss appear to be the primary factors contributing to the increased cost of submerged swimming in ducks and cormorants. This is also supported by the analyses of Grémillet et al. (1998), who have emphasized that the minimization of plumage air in cormorants represents a balance between the costs of increased buoyancy *versus* increased heat loss.

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