

EMPEROR PENGUIN OXYGEN CONSUMPTION, HEART RATE AND PLASMA LACTATE LEVELS DURING GRADED SWIMMING EXERCISE

G. L. KOOYMAN AND P. J. PONGANIS

*Centre for Marine Biotechnology and Biomedicine, Scripps Institution of
Oceanography, University of California, San Diego, La Jolla, CA 92093, USA*

Accepted 1 June 1994

Summary

Oxygen consumption (\dot{V}_{O_2}), heart rate and blood chemistry were measured in four emperor penguins, *Aptenodytes forsteri* (Gray), during graded swimming exercise. The maximum \dot{V}_{O_2} obtained, $52 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, was 7.8 times the measured resting \dot{V}_{O_2} of $6.7 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ and 9.1 times the predicted resting \dot{V}_{O_2} . As the swimming effort rose, a linear increase in surface and submerged heart rates (*fh*) occurred. The highest average maximum surface and submersion heart rates of any bird were 213 and 210 beats min^{-1} , respectively. No increase in plasma lactate concentrations occurred until \dot{V}_{O_2} was greater than $25 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$. At the highest \dot{V}_{O_2} values measured, plasma lactate concentration reached 9.4 mmol l^{-1} . In comparison with other animals of approximately the same mass, the aerobic capacity of the emperor penguin is less than those of the emu and dog but about the same as those of the seal, sea lion and domestic goat. For aquatic animals, a low aerobic capacity seems to be consistent with the needs of parsimonious oxygen utilization while breath-holding.

Introduction

Maximum oxygen consumption ($\dot{V}_{O_{2\text{max}}}$) has not been measured in birds, but \dot{V}_{O_2} is about 10–13 times the resting rate during horizontal flight (LeFebvre, 1964; Tucker, 1968; Butler *et al.* 1977) and is over 15 times the resting rate in hovering hummingbirds (Lasiewski, 1963). In contrast, ducks swimming in a watermill can only increase their \dot{V}_{O_2} about 3.5–4 times above out-of-water resting rates (Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983; Baudinette and Gill, 1985; Butler, 1991). The low \dot{V}_{O_2} increases for swimming ducks are due to the small amount of leg muscle required for propulsion, compared with the larger flight muscles (Prange and Schmidt-Nielsen, 1970; Butler, 1991). Since penguins ‘fly’ under water, they use a much greater amount of their muscle mass than do swimming ducks and may, therefore, have a metabolic scope closer to that of flying birds. However, it would seem that diving birds, such as the emperor penguin, would be metabolically adapted to O_2 conservation and would consequently have a moderate aerobic scope, similar to that measured in seals (Ponganis *et al.* 1990a)

Key words: lactate, oxygen consumption, heart rate, *Aptenodytes forsteri*.

and sea lions (Ponganis *et al.* 1991; Williams *et al.* 1991). Furthermore, the exceptionally low drag of their fusiform body shape (Nachtigall and Bilo, 1980) suggests that penguins may swim at low energetic costs even at high speeds.

We selected emperor penguins, the largest of all aquatic birds, so that we would be able to make comparisons, at high swimming effort, with marine mammals of similar mass that have already been studied within the same type of exercise protocol. This comparison was, in part, prompted by the diving physiology and behaviour of emperor penguins. During dives, heart rate responses of emperor penguins are similar to those observed in phocid seals (Kooyman *et al.* 1992b). However, for their size, birds appear to be better divers if duration, depth and speed are used as the evaluating criteria. Emperor penguins cruise at a speed about 50% faster than those of seals and sea lions (Ponganis *et al.* 1990b; Castellini *et al.* 1992; Kooyman *et al.* 1992b). King penguins (*Aptenodytes patagonicus*) often dive for longer than 5 min, to depths greater than 200 m, and at speeds of slightly more than 2 m s^{-1} (Kooyman *et al.* 1992a); emperor penguin diving capacities are about twice those of king penguins (G. L. Kooyman, unpublished observations). In an analysis of several fur seal species, none matched any of these diving standards even though all were at least two times greater in body mass (Gentry and Kooyman, 1986).

We therefore sought to measure the metabolic scope, exercise heart-rate response and alteration in plasma lactate concentration in emperor penguins (*Aptenodytes forsteri*) during graded exercise. These variables provided us with the information needed to determine whether the birds were near or at $\dot{V}_{\text{O}_2\text{max}}$. The results show a close correlation between average heart rate and average \dot{V}_{O_2} . The reluctance or inability of the birds to swim beyond the maximum induced work load and the rapid rise in plasma lactate concentration at this inflection point indicate that an aerobic/anaerobic threshold had been reached. This level of exercise was similar to that at the highest \dot{V}_{O_2} measured previously in seals, sea lions and dolphins (Ponganis *et al.* 1990a, 1991; Williams *et al.* 1991, 1993).

Materials and methods

Husbandry

On 12 November 1988, four 4-month-old emperor penguin chicks (CW, M, T, N) weighing between 2.5 and 4.5 kg were collected at Cape Washington ($74^{\circ}39'S$, $167^{\circ}22'E$), Antarctica. They were flown by twin-otter aircraft to a sea-ice laboratory near McMurdo Station. After 6 days at the station, they were flown directly to San Diego, California, in a refrigerated US Air Force Starlifter. Brief stops were made at Christchurch, New Zealand, and Honolulu, Hawaii. Within 24 h, the birds were placed in the Sea World polar bird quarantine facility (Mission Bay, San Diego, California). In this environment, they were hand-fed until they were transferred to the Sea World public display facility. The air temperature in the display was 2°C and the water temperature was about 5.5°C .

Resting \dot{V}_{O_2} was measured in three birds when they were 1 year old. One bird (N) did not moult in the normal cycle, so it was not used in the heart-rate experiments. The exercise experiments were conducted when the birds were between 1.5 and 2.5 years old. During that period, the birds weighed between 19.9 and 26.7 kg.

For each experiment, the birds were transported to Scripps Institution of Oceanography (SIO), University of California, San Diego (UCSD), in upright, padded boxes in a refrigerated van. They remained in the van except when an experiment was conducted. Total time away from Sea World was between 36 and 48 h for each trip.

At the SIO Hydraulics Laboratory, UCSD, the birds were placed individually in the water channel previously described by Davis *et al.* (1985). All procedures for measuring \dot{V}_{O_2} , increasing the workload (swim effort) and measuring heart rate were the same as formerly described (Davis *et al.* 1985; Ponganis *et al.* 1990a; Williams *et al.* 1991). Very briefly, water in the water channel (1.1 m square \times 16 m long) was chilled to 2–4 °C the day before the experiment. This water temperature was about the same as that at the Sea World facility. Water flow rate was held constant at 1 m s⁻¹ while the birds swam in a 2.5 m long test section partitioned by two grates from the rest of the channel.

Water velocity was measured with an electromagnetic flow sensor placed 30 cm above the floor of the flume. A vertical profile of water velocity varied by less than 0.1 m s⁻¹ (Davis *et al.* 1985). The velocity was correlated to the rotation rate of the propellers, which in normal operation was used to set the water speed. Water velocity in the test section was the same as in the rest of the channel.

Metabolic rate

Resting \dot{V}_{O_2} was obtained from three birds held for several hours in a small water bath, temperature regulated at 1.5–6.1 °C. During exercise in the water channel, the swim procedure and \dot{V}_{O_2} measurements were as follows. Before releasing a bird into the flume, a narrow epoxy-glue strip painted on the mid-line of the back and about two-thirds of the body length from the head was used as an anchor for attachment of a 5 cm long, 1.5 cm diameter tube to the feathers with nylon ties. The tube had a swivel to prevent an attached load line from becoming twisted when the bird occasionally made turns. The 6 mm diameter, braided nylon line passed through the rear grate in the centre of the channel and made an approximately 45° turn through a pulley towards the surface. About 1 m above the surface, the line turned vertically through another pulley hanging at the edge of the channel. About 2 m below this second pulley, the desired weight was hung onto the line. A weight of at least 0.25 kg was always applied, to prevent slack in the line. This arrangement produced a horizontal pull on the penguin when it swam in the centre of the channel. Increased swim effort was produced by adding loads ranging from 0.25 to 4 kg.

Once the bird had been released in the test section, the water surface was covered with an acrylic dome mounted on a sheet of 6 mm plywood. The birds breathed under this dome, and air was drawn through the dome at a suitable rate to maintain the O₂ concentration above 20%. Air flow, O₂ concentration, calibration of the system and calculation of \dot{V}_{O_2} were accomplished with an on-line computer system similar to that described by Davis *et al.* (1985).

Experiments in which the heaviest loads (3–4 kg) were added lasted for about 3 min, and \dot{V}_{O_2} was determined every 10 s. Experiments at these high loads ended when the birds showed signs of fatigue. A plateau of values within the range $\pm 15\%$ of average was short, or not found. Experiments with lighter loads lasted for about 30 min and soon after they

began, \dot{V}_{O_2} reached a plateau and remained stable until the end. Average \dot{V}_{O_2} values were determined from the sum of all values from all runs at a specific load. During heart rate and lactate experiments, average \dot{V}_{O_2} values were calculated from the \dot{V}_{O_2} measurements during the specific run in which the heart rate or lactate determination was made.

Heart rate

Prior to f_H and lactate measurements, the birds were anaesthetized. The procedure used was similar to that described previously (Kooyman *et al.* 1992b). In brief, birds were masked with a 1 l plastic bottle in which a neoprene neck ring formed a seal. Induction was at 4% isoflurane, which was reduced to 1% during the procedure.

For placing heart-rate electrodes, anaesthesia lasted about 30 min, and after about 5 h of recovery the bird was released into the flume. As in previous studies (Kooyman *et al.* 1992b), the two electrodes were placed on the dorsal midline; one was placed between the wings and another about two-thirds of the body length behind the head. Heart rates were monitored on a Hewlett-Packard chart recorder. The total heart beat count of each surface and submersion interval was divided by the duration of the interval to obtain f_H . The average f_H for a specific \dot{V}_{O_2} was calculated by summing all beats over the entire exercise cycle and dividing by the total time. Heart rate analysis was performed only for periods in which \dot{V}_{O_2} was stable. Surface and submersion times were manually recorded by an observer and stored on the computer as \dot{V}_{O_2} was measured.

Lactate levels

The placement of catheters required 30–60 min under anaesthesia. An 18 gauge (1.3 mm diameter, 3 cm length) catheter was placed 2.5 cm into the vein of the middle toe. The catheter was held in place with Vetwrap coated with epoxy glue to form a rigid cast that allowed the foot enough mobility for normal positioning while swimming. A 2 m extension was placed on the catheter, the dead space of which was 1.6 ml. This length was necessary to raise the sampling stopcock above the water for sampling during swimming. Sampling duration ranged from 30 s to 10 min and was fastest when the bird was swimming and slowest between runs, when the bird rested in the water and was usually shivering. Samples were analyzed immediately after collection on a YSI model 2300 Stat lactate and glucose analyzer. Heart-rate and blood-sampling experiments were carried out separately to avoid catheter, electrode and load lines becoming tangled when the birds made turns in the flume.

Statistics

All statistics and tests of significance were obtained using the Statistix commercial software package (St Paul, MN). Unless stated otherwise, confidence intervals are expressed as one standard deviation of the mean.

Results

Resting \dot{V}_{O_2} values were measured during quiet periods in the water-bath metabolic chamber (Fig. 1, Table 1). The lowest \dot{V}_{O_2} was $6.2 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ for individual CW when the water temperature was 1.5°C .

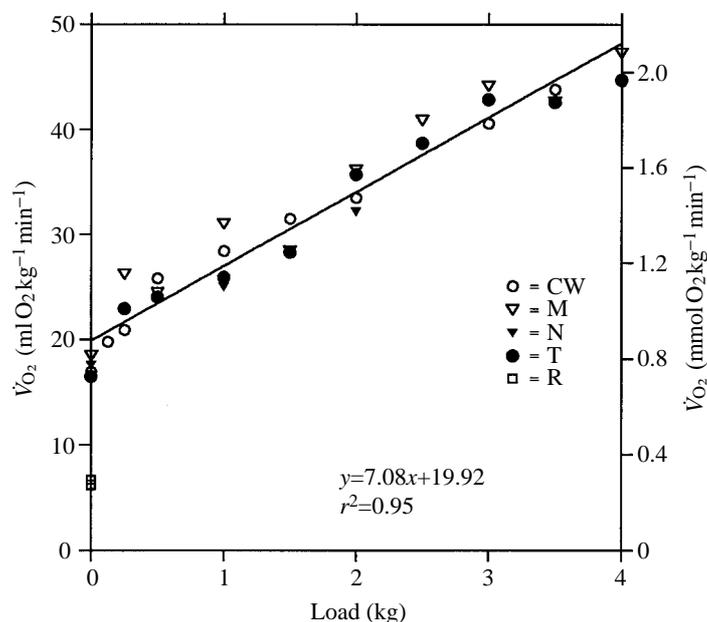


Fig. 1. Measured $\dot{V}O_2$ of all birds in relation to load. Average resting values from Table 1 are indicated as upright triangles. Other symbols are for the overall average $\dot{V}O_2$ at each load for each bird. Standard errors of the means fall within the symbols.

Table 1. Resting $\dot{V}O_2$; samples were taken every 10 s

Bird	Minimum resting $\dot{V}O_2$ (ml O ₂ kg ⁻¹ min ⁻¹)	Water temperature (°C)	N
CW	6.2±0.99	1.5	115
M	6.7±1.89	2.4	221
T	6.7±2.09	6.1	185

Values are ± one standard deviation.

During exercise, $\dot{V}O_2$ was closely correlated with load, and the coefficients of determination (r^2) ranged from 0.93 to 0.99. There was no significant difference among the birds either in the slope or the intercept (analysis of covariance, multiple-comparison test, $P < 0.05$; Zar, 1984). The pooled analysis is shown in Fig. 1.

The maximum mean $\dot{V}O_2$ when loaded was 47.3 ml O₂ kg⁻¹ min⁻¹ for M while swimming and pulling a 4 kg load. Maximum values for both CW and T were close to this, at 44.6 ml O₂ kg⁻¹ min⁻¹ and 44.7 ml O₂ kg⁻¹ min⁻¹ respectively, also with a 4 kg load (Fig. 1). The maximum average value for a single run was 52 ml O₂ kg⁻¹ min⁻¹ for M (Figs 2 and 3).

Heart rates

Regression lines for the relationship between f_H and $\dot{V}O_2$ during surface swimming and

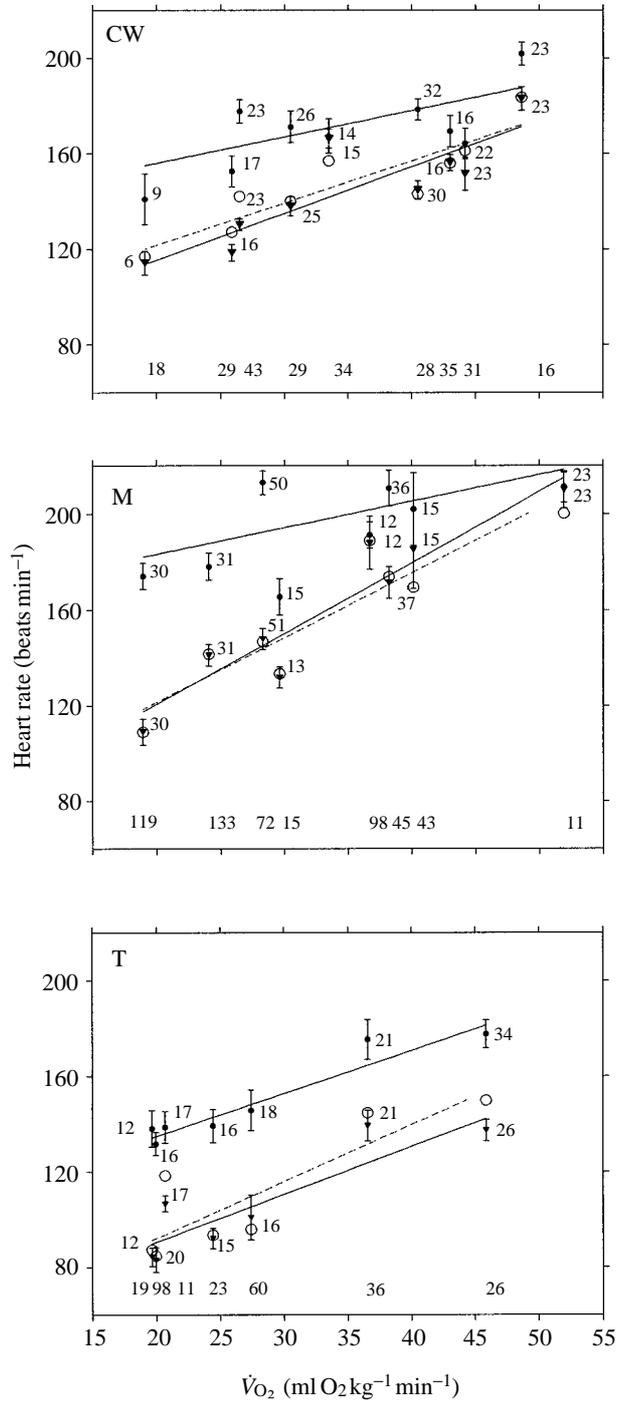


Fig. 2

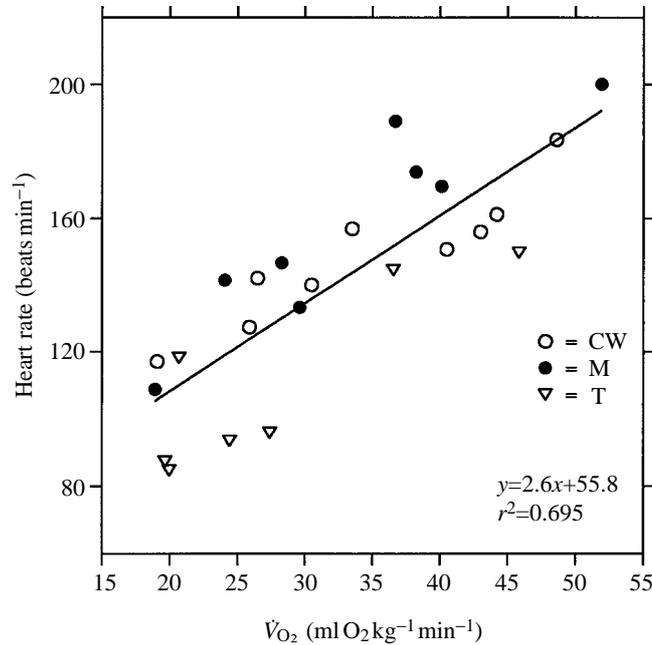


Fig. 3. The relationship between mean heart rate and mean $\dot{V}O_2$ at all exercise levels for the three birds. These values are the same as the open circles in each part of Fig. 2.

submersion are summarized in Fig. 2 and Table 2. The r^2 values ranged from 0.07 for M when surfaced to 0.39 for CW and T when submerged. In all three birds, examination of surface *versus* submerged f_H values showed that mean f_H values at the surface and while submerged were significantly different ($P < 0.001$, paired sample t -test, d.f.=23). These mean surface and submerged f_H values are given in Fig. 2. Submersion times ranged from 5 to 15 s; the lowest values corresponded to the highest $\dot{V}O_2$ values. Surface times ranged from 2 to 6 s. The average heart rate values at specific $\dot{V}O_2$ values for each bird are plotted in Fig. 2 for each bird and in Fig. 3 for pooled results.

Plasma lactate levels

The highest lactate levels were 7 and 9.5 mmol l⁻¹ in birds CW and M, respectively. Fig. 4 shows the relationship between [lactate] and swimming $\dot{V}O_2$.

Fig. 2. Submersion and surface heart rates in relation to $\dot{V}O_2$ in three swimming penguins. The dashed regression line was calculated from the mean heart rate and $\dot{V}O_2$ for each run (open circles). Mean surface (filled circles) and submersion (filled triangles) heart rates for all runs were calculated from all surface and submersion rates during each run. The bars show ± 1 standard error. $\dot{V}O_2$ values are the means for each run for which the heart rates were measured. Standard errors fall within the symbols. Values next to each point represent the number of surface and submersion intervals during which heart rate was measured for each run. Numbers above the $\dot{V}O_2$ axis are the number of 10 s samples used to determine mean $\dot{V}O_2$ values.

Table 2. Values for the regressions of heart rate (f_H ; beats min^{-1}) on oxygen consumption (\dot{V}_{O_2} ; $\text{ml O}_2 \text{kg}^{-1} \text{min}^{-1}$) during graded swim effort

Bird	Surfaced				Submerged				Average			
	a	b	r^2	N	a	b	r^2	N	a	b	r^2	N
CW	134	1.1	0.09	182	77	1.9	0.39	177	87	1.7	0.79	9
M	161	1.1	0.07	214	62	2.9	0.38	212	68	2.7	0.85	8
T	99	1.8	0.23	134	51	2.0	0.39	127	45	2.4	0.74	7

The equation is $y=a+bx$, where y is f_H , x is \dot{V}_{O_2} .

N refers to the number of surface and submergence intervals during which heart rate was calculated.

In the average f_H equation, N is equal to the number of determinations of average \dot{V}_{O_2} .

All r^2 values are significant at $P=0.05$.

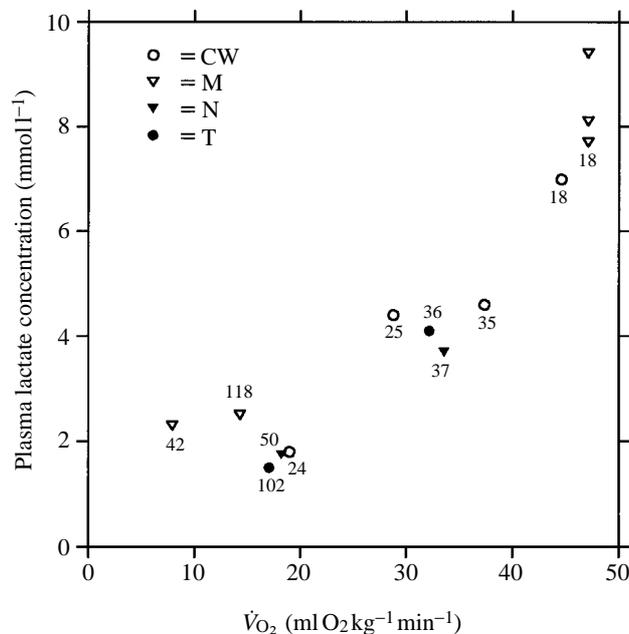


Fig. 4. The relationship between maximum plasma lactate concentration and the mean \dot{V}_{O_2} determined when the lactate sample was drawn. Numbers above and below the symbols are the number of 10 s samples used to determine mean \dot{V}_{O_2} values.

Discussion

The 10- to 13-fold increase in \dot{V}_{O_2} from resting levels during flight in birds previously cited should not be assumed to represent the entire aerobic scope of birds since $\dot{V}_{O_{2max}}$ was not measured. Similarly, the highest measured \dot{V}_{O_2} in this study ($52 \text{ ml O}_2 \text{kg}^{-1} \text{min}^{-1}$) may not represent $\dot{V}_{O_{2max}}$ for the emperor penguin, since no plateau in \dot{V}_{O_2} occurred. However, the observers' impressions of the swimming effort of the birds when pulling a 4 kg load, as well as the high plasma lactate concentration (Fig. 4) at these loads, suggested that the birds were near their maximum limit. The

lowest measured resting \dot{V}_{O_2} of $6.2 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ is similar to previous values obtained for emperor penguins resting in air in their thermoneutral zone ($6.2\text{--}7.3 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$; Pinshow *et al.* 1976; Le Maho *et al.* 1976; Deswasmes *et al.* 1980). This is greater than the resting rate of $5.7 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ for a 20.8 kg bird predicted from the equation given by Aschoff and Pohl (1970). The metabolic scope of the emperor penguin, from our values, is 7.8, and it is 9.1 using the predicted resting \dot{V}_{O_2} .

The maximum increase in \dot{V}_{O_2} measured in swimming emperor penguins is less than that measured in birds during flapping flight. However, all flying birds are considerably smaller than emperor penguins (Butler, 1991), so that direct comparisons are difficult. The emu (*Dromaius novaehollandiae*) is of similar body mass to the emperor penguin, and the highest measured \dot{V}_{O_2} for this bird ($48 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) and the resting \dot{V}_{O_2} ($4.2 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) gave a metabolic scope of 11.4 (Grubb *et al.* 1983). As $\dot{V}_{O_{2\text{max}}}$ was not measured, the actual aerobic capacity of the emu is therefore probably much greater than that of the emperor penguin.

The aerobic capacity of the emperor penguin measured in this study is, therefore, lower than that for the running emu or for flying birds. Patak and Baldwin (1993) recently reported that the relative mass and oxidative capacity of the pelvic limb muscle of emus were similar to those of the flight muscles of birds. Although the emperor penguin pectoralis/supracoracoideus muscle mass constitutes a similar percentage of the body mass (P. J. Ponganis, unpublished results) to that of the pelvic limb muscle of the emu (Patak and Baldwin, 1993), muscle oxidative capacity may be less, as previous studies have suggested that emperor penguin muscle is 'best adapted for anaerobic work' (Baldwin, 1988). Its lower aerobic capacity in comparison with the emu and with flying birds may, therefore, be related more to differences in mitochondrial density than to relative muscle mass.

The measured exercise capacity of the emperor penguin is also less than the 30- and 12-fold aerobic scopes of dogs and goats, terrestrial mammals of similar body mass to emperor penguins (Taylor *et al.* 1987). Those values were based on measured $\dot{V}_{O_{2\text{max}}}$ data and predicted resting \dot{V}_{O_2} values. The ninefold increase in emperor penguin \dot{V}_{O_2} above predicted resting levels is, however, similar to that measured in three marine mammals. Maximum \dot{V}_{O_2} measured in the bottlenose dolphin (*Tursiops truncatus*) was 7–11 times the predicted resting rate (Williams *et al.* 1993). In harbour seals (*Phoca vitulina*) and sea lions (*Zalophus californianus*), both of similar mass to the emperor penguin, the maximal measured exercise capacity was 9–10 times both the predicted and measured resting \dot{V}_{O_2} (Ponganis *et al.* 1990a, 1991). Although we did not obtain a well-defined $\dot{V}_{O_{2\text{max}}}$, the measured aerobic capacity of the emperor penguin appears to be most similar to the aerobic capacities measured in diving mammals.

The surface and submersion heart rates during surface swimming of emperor penguins (Fig. 2) were much higher than those during diving (Kooyman *et al.* 1992b), and both increased with workload in a manner similar to that found in sea lions (Williams *et al.* 1991). Mean f_H also increased with \dot{V}_{O_2} (Fig. 3), as in both harbour seals and sea lions (Williams *et al.* 1991; Butler *et al.* 1992). The f_H of emperor penguins is similar to that of seals and sea lions when the \dot{V}_{O_2} is at the same level

(Williams *et al.* 1991; Butler *et al.* 1992). However, the highest \dot{V}_{O_2} levels reported for these mammals was 20–25 ml O₂ kg⁻¹ min⁻¹. Seals and sea lions show a significant drop in f_H between surface breathing and when submerged; in the seal, submersion f_H is about one-third of the surface rate (Ponganis *et al.* 1990a). The surface and submersion f_H pattern of the emperor penguin is similar to that of the seal, although absolute f_H values were higher.

It was not possible to estimate swimming speeds from the methods used in this study. Flow was turbulent because of the grate, and thrust generation by the wings while swimming in natural conditions may be different from thrust generation while swimming against flowing water in a channel or against flowing water with a load applied. Thus, direct extrapolation of diving in the wild may be limited. Comparisons between video tapes of penguins swimming in the wild and in the channel showed that the amplitude and frequency of the wing stroke appeared to be lower under natural conditions than for the captive birds swimming with the lightest load. Wing-beat frequency of emperor penguins swimming in the wild was about 45 beats min⁻¹ (G. L. Kooyman unpublished), and an average of 62–70 beats min⁻¹ for captive birds swimming with the lightest loads. Similarly, heart rates during natural dives (Kooyman *et al.* 1992b) are often less than the submerged heart rates observed at the lowest workloads in this study. Therefore, it seems reasonable to assume that \dot{V}_{O_2} of diving birds in the wild would be less than the lowest submerged swimming values obtained in this study, 20 ml O₂ kg⁻¹ min⁻¹ (Fig. 1). If so, then the emperor penguin diving metabolic rate would be less than three times the resting levels we measured, which is less than the swimming \dot{V}_{O_2} of six times the resting metabolic rate measured in the Adelie penguin (*Pygoscelis adeliae*) surface swimming in a 20 m water channel at 2.3 m s⁻¹ (Culik and Wilson, 1991). Such a diving metabolic rate would be consistent with the moderate aerobic capacity measured in this study and may help to explain the emperor penguin's remarkable diving breath-hold capacity of 15–20 min (Kooyman *et al.* 1971).

We thank L. Starke, L. Winter, P. Jobsis and S. Eckert for assistance in these studies. This research was supported by grants NSF DPP 87-15863 and USPHS HL 17731.

References

- ASCHOFF, S. AND POHL, H. (1970). Rhythmic variation in energy metabolism. *Fedn. Proc. Fedn Am. Socs. exp. Biol.* **29**, 1541–1552.
- BALDWIN, J. (1988). Predicting the swimming and diving behavior of penguins from muscle biochemistry. *Hydrobiologia* **165**, 255–261.
- BAUDINETTE, R. V. AND GILL, P. (1985). The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *J. comp. Physiol.* **155**, 373–380.
- BUTLER, P. J. (1991). Exercise in birds. *J. exp. Biol.* **160**, 233–262.
- BUTLER, P. J., WEST, N. H. AND JONES, D. R. (1977). Respiratory and cardiovascular responses of the pigeon to sustained level flight in a wind-tunnel. *J. exp. Biol.* **71**, 7–26.
- BUTLER, P. J., WOAKES, A. J., BOYD, I. L. AND KANATOUS, S. (1992). Relationship between heart rate and oxygen consumption during steady-state swimming in California sea lions. *J. exp. Biol.* **170**, 35–42.
- CASTELLINI, M. A., KOOYMAN, G. L. AND PONGANIS, P. J. (1992). Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. exp. Biol.* **165**, 181–194.

- CULIK, B. AND WILSON, R. P. (1991). Energetics of under-water swimming in Adelie penguins. *J. comp. Physiol. B* **161**, 285–291.
- DAVIS, R. W., WILLIAMS, T. M. AND KOOYMAN, G. L. (1985). Swimming metabolism of yearling and adult harbor seals (*Phoca vitulina*). *Physiol. Zool.* **58**, 590–596.
- DESWASMES, G., LE MAHO, Y., CORNET, A. AND GROSCOLO, R. (1980). Resting metabolic rate and cost of locomotion in long-term fasting emperors. *J. appl. Physiol.* **49**, 888–896.
- GENTRY, R. L. AND KOOYMAN, G. L. (eds) (1986). *Fur Seals: Maternal Strategies on Land and at Sea*. New Jersey: Princeton University Press. 291pp.
- GRUBB, B., JORGENSEN, D. O. AND CONNER, M. (1983). Cardiovascular changes in the exercising emu. *J. exp. Biol.* **109**, 193–201.
- KOOYMAN, G. L., CHEREL, Y., LE MAHO, Y., CROXALL, J. P., THORSON, P. H., RIDOUX, V. AND KOOYMAN, C. A. (1992a). Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* **62**, 143–163.
- KOOYMAN, G. L., DRABEK, C. M., ELSNER, R. AND CAMPBELL, W. B. (1971). Diving behavior of the emperor penguin, *Aptenodytes forsteri*. *Auk* **88**, 775–795.
- KOOYMAN, G. L., PONGANIS, P. J., CASTELLINI, M. A., PONGANIS, E. P., PONGANIS, K. V., THORSON, P. H., ECKERT, S. A. AND LE MAHO, Y. (1992b). Heart rates and swim speeds of emperor penguins diving under sea ice. *J. exp. Biol.* **165**, 161–180.
- LASIEWSKI, R. C. (1963). Oxygen consumption of torpid, resting, active and flying hummingbirds. *Physiol. Zool.* **36**, 122–140.
- LEFEBRE, E. A. (1964). The use of D₂O¹⁸ for measuring metabolism in *Columbia livia* at rest and in flight. *Auk* **81**, 403–418.
- LE MAHO, Y., DECLITTE, R. AND CHATONNET, J. (1976). Thermoregulation in fasting emperor penguins under natural conditions. *Am. J. Physiol.* **231**, 913–922.
- NACHTIGALL, W. AND BILO, D. (1980). Stromungsanpassung des Penguins beim Schwimmen unter wasser. *J. comp. Physiol.* **137**, 17–26.
- PATAK, A. AND BALDWIN, J. (1993). Structural and metabolic characterization of the muscles used to power running in the emu (*Dromaius novae-hollandiae*), a giant flightless bird. *J. exp. Biol.* **175**, 233–249.
- PINSHOW, B., FEDAK, M. A., BATTLES, D. R. AND SCHMIDT-NIELSEN, K. (1976). Energy expenditure for thermoregulation and locomotion in emperor penguins. *Am. J. Physiol.* **231**, 903–912.
- PONGANIS, P. J., KOOYMAN, G. L. AND ZORNOW, M. H. (1991). Cardiac output in swimming california sea lions, *Zalophus californianus*. *Physiol. Zool.* **64**, 1296–1306.
- PONGANIS, P. J., KOOYMAN, G. L., ZORNOW, M. H., CASTELLINI, M. A. AND CROLL, D. A. (1990a). Cardiac output and stroke volume in swimming harbor seals. *J. comp. Physiol.* **160**, 473–482.
- PONGANIS, P. J., PONGANIS, E. P., PONGANIS, K. V., KOOYMAN, G. L., GENTRY, R. L. AND TRILLMICH, F. (1990b). Swimming velocities in otariids. *Can. J. Zool.* **68**, 2105–2112.
- PRANGE, H. D. AND SCHMIDT-NIELSEN, K. (1970). The metabolic cost of swimming in ducks. *J. exp. Biol.* **53**, 763–777.
- TAYLOR, C. R., KARAS, R. H., WEIBEL, E. R. AND HOPPELER, H. (1987). Adaptive variation in the mammalian respiratory system in relation to energetic demand. II. Reaching the limits to oxygen flow. *Respir. Physiol.* **69**, 7–26.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67–87.
- WILLIAMS, T. M., FRIEDL, W. A. AND HAUN, J. E. (1993). The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *J. exp. Biol.* **179**, 31–46.
- WILLIAMS, T. M., KOOYMAN, G. L. AND CROLL, D. A. (1991). The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. comp. Physiol.* **160**, 637–644.
- WOAKES, A. J. AND BUTLER, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. exp. Biol.* **107**, 311–329.
- ZAR, J. H. (1984). *Biostatistical Analysis*. Englewood, NJ: Prentice Hall. 718pp.