

HEART RATES AND SWIM SPEEDS OF EMPEROR PENGUINS DIVING UNDER SEA ICE

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Summary

Heart rate during overnight rest and while diving were recorded from five emperor penguins with a microprocessor-controlled submersible recorder. Heart rate, cardiac output and stroke volume were also measured in two resting emperor penguins using standard electrocardiography and thermodilution measurements. Swim velocities from eight birds were obtained with the submersible recorder. The resting average of the mean heart rates was 72 beats min⁻¹. Diving heart rates were about 15 % lower than resting rates. Cardiac outputs of 1.9–2.9 ml kg⁻¹ s⁻¹ and stroke volumes of 1.6–2.7 ml kg⁻¹ were similar to values recorded from mammals of the same body mass. Swim velocities averaged 3 ms⁻¹. The swim speeds and heart rates suggest that muscle O₂ depletion must occur frequently: therefore, many dives require a significant energy contribution from anaerobic glycolysis.

Introduction

If the term 'diving' is restricted to those swim activities in which an animal is voluntarily submerging itself under natural or quasi-natural conditions, then there have been few physiological studies of diving in aquatic animals. Most 'diving'

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experiments have been carried out with a protocol in which the animal is restrained and forcibly submerged. These forced submersions have been studied extensively and are the subject of several reviews (Butler and Jones, 1982; Blix and Folkow, 1983; Elsner and Gooden, 1983; Kooyman, 1989). In aquatic mammals, the animals show a consistent pattern of a marked bradycardia, reduced cardiac output and stroke volume, restricted blood flow to the periphery and, upon recovery, a rapid increase in blood lactic acid level. During forced submersions, cardiovascular responses of birds are less consistent. In a detailed review, it has been described how mallard ducks and a dabbling duck show a slow bradycardic response in which a marked decline does not occur until there is adequate stimulation of chemoreceptors (Butler and Jones, 1982). In contrast, the tufted duck, a diving duck (Butler and Woakes, 1982), cormorants (Mangalam and Jones, 1984) and penguins (Kooyman, 1989) show an immediate bradycardia when they are submerged. Other features, such as reduced peripheral blood flow and post-submersion rise in blood lactic acid levels, are similar to those in mammals (Jones *et al.* 1979; Scholander, 1940).

There have been no physiological studies of birds diving under natural conditions; all have been restricted to small pools and short, shallow dives which most closely simulate natural conditions of diving ducks (Woakes and Butler, 1983). In order to obtain information on diving physiology under natural conditions, we elected to study emperor penguins *Aptenodytes forsteri* for the following reasons. (1) The size and robustness of the bird is compatible with the recorders we wished to use in the study. (2) The birds are abundant, easily captured and exceptionally tractable. (3) They are the largest of all diving birds and their known deep-diving ability suggests that they have the greatest breath-hold capacities of birds. Such capacity means that physiological variables related to breath-hold diving could be measured over a relatively long time, allowing responses to stabilize. (4) Most importantly, their habitat is ideal for diving physiology studies in the same way that the Weddell seal has been greatly utilized for such studies (Kooyman, 1981, 1989; Zapol, 1987). That is, they readily dive under large, unbroken plates of sea ice that are several meters thick. The habitat conditions are described in more detail below.

Our objectives were to measure (1) cardiac output and stroke volume in resting birds; (2) heart rate in birds while resting and diving; and (3) swim velocities from the same birds under conditions similar to those during the heart rate experiments. In some instances, we were able to obtain both heart rate and swim velocity simultaneously. Our goal was to compare these results with previous studies on penguins and marine mammals. Because the dives would be longer and deeper than previous studies on birds and because the emperor penguin is the largest of the diving birds, we hypothesized that the heart rates would be lower than in previous studies. Conversely, since the emperor penguin is much smaller than the marine mammals studied so far, we expected higher average heart rates than in seals. Swim speed has not been scaled to body size, but we intuitively presumed slower velocities in birds since drag is related to body surface area or frontal area

and muscle mass. Since the power source scales to the cube of body length, we presumed that shorter animals would have a proportionally smaller muscle mass.

Materials and methods

Capture and husbandry

Birds were obtained from groups that leave the ice edge and wander south towards McMurdo Station. In both 1987 and 1988, the birds were collected as one of these groups passed near our sea-ice laboratory. In 1987 we collected four birds and held them in a snow fence corral for 28 days. Each bird was marked by clipping the outer part of the feathers in a distinct area that would be visible when they were under water. Sex was determined by their trumpeting call (Prevost, 1961). Mass was obtained by weighings on a platform spring scale. In 1988, 10 birds were herded into a corral and 6 were held for 48 days while the other 4 were released a few days after capture. Similar means of identification were used as in 1987, but weighings were made on a Doran load cell (model 7000) when the birds were unconscious during anesthesia or as they walked through a narrow chute on their way to or from the diving hole. The diving hole was a 1.2 m by 2 m hole drilled through the sea ice with a 1.2 m ice augur.

Although the birds were catching fish while they dived through the ice hole, we supplemented their diet with locally caught fish as well as fish imported from New Zealand. Initially they lost weight but they gained weight after learning to eat from hand offerings. Their mass was similar to that of emperor penguins that were free at this time of the year (Table 1).

Experimental setting

In 1987 the diving hole and laboratory were about 1 km offshore on ice 2 m thick that had no platelet layer under the firm ice, and the water depth was about 400 m. Other exit holes were available as indicated in Fig. 1A. These holes were shared with Weddell seals, one of which was an exceptionally aggressive male that not only attacked any other seals that came into the area but occasionally chased the penguins. We noted from underwater observations that the penguins both out-manuevered and swam faster than the seal. The seal was moved eventually to another site for physiological experiments.

In 1988, the corral was larger than in 1987. It was 6 km offshore, the ice was 3 m thick with a platelet layer of about 2 m, and water depth was 620 m. Because of the ice thickness and the snow cover, it was much darker under the ice, but it did not inhibit the birds in any noticeable way. There were no stray seals at this site.

At first in 1987, the birds were allowed in the water only when there was an observer in the observation chamber so that the behavior of the penguins could be monitored constantly. The birds were never forced into the water; a gate to the hole was simply opened and the birds dived when ready.

The hole arrangement was different in 1988 (Fig. 1B), and the diving procedure was also modified. Often the birds were allowed to dive any time they wished, day

Table 1. *Summary of basic information on birds studied*

Bird number	Sex	Date of capture	Date of release	Mass (kg)			Heart rate		Cardiac output
				Capture	Release	Resting	Diving	Speed	
1-87	—	11/10/87	12/8/87	23.6	24.5	X	X		
2-87	—	”	”	20.8	20.9	X	X	X	
3-87	—	”	”	20.9	23.2	X	X		
1-88	M	10/26/88	12/13/88	24.2	28.6	X	X		
2-88	F	”	”	23.1	25.0			X	
3-88	—	”	”	24.6	26.7			X	
4-88	—	”	”		26.6			X	
6-88	M	”	11/11/88	21.2					X
8-88	M	”	12/13/88	21.8	26.0			X	
9-88	—	”	”	19.9	23.7	X	X	X	
2-89	—	10/17/89	10/22/89	20.3					X
			Mean	22.7	25.0				
			S.D.	1.68	2.27				

An X means the bird participated in the experiment.

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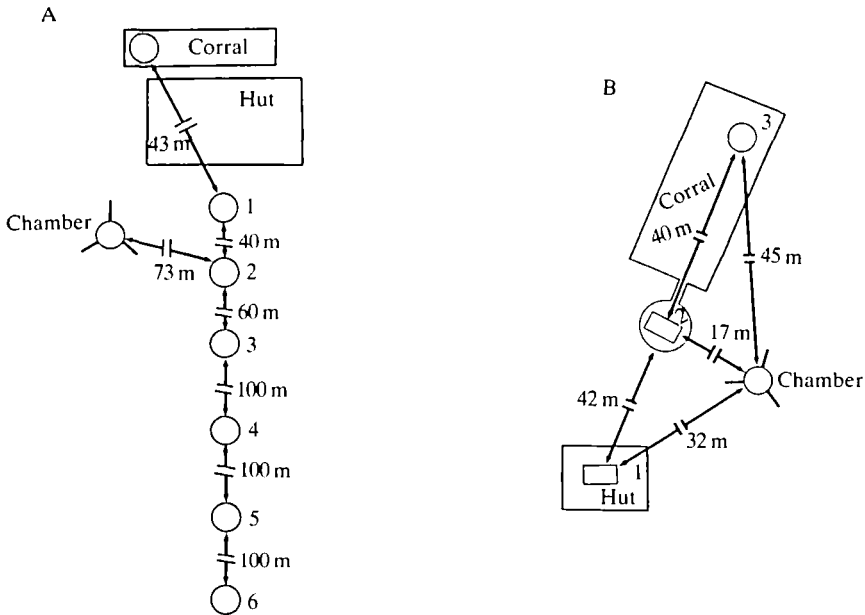


Fig. 1. (A) Configuration of the experimental hut, observation chamber, dive holes and corral in 1987. The main dive hole was in the corral. All other holes were open or closed at different periods. After a short time, holes 4, 5 and 6 were closed permanently. (B) Configuration of the experimental area in 1988. The primary dive hole was 2. During the early stages of the study, hole 3 was opened frequently, but later it was closed permanently.

or night. We always knew when the birds were going to dive because they would gather at the hole for a few minutes and engage in what we called a 'conference'. When water entry was imminent, they would hyperventilate for a few breaths. A dive was almost always followed by leaving the water for a recovery that lasted a few minutes before the next dive.

Anesthesia

Most of the studies required an initial general anesthesia to prepare the bird for the experiment. For example, the birds were anesthetized to place a recorder mount on the back as well as to attach the subcutaneous electrodes for recording heart rate. The recorder mount consisted of a 2 cm × 15 cm long epoxy glue patch on the outer tips of the feathers. The microprocessor was placed on the glue patch and secured with nylon ties. The recorder was easily placed on and removed from the bird while it was distracted with fish. No restraint was required. The glue base was peeled off at the end of the study when the birds were released.

General anesthesia was administered with a standard semi-closed anesthesia circuit and 100 % oxygen. Induction of anesthesia with 3–4 % isoflurane was accomplished by placing a 2 l cylindrical mask over the bird's head. An anesthetic

level was maintained with 1–2 % isoflurane and spontaneous ventilation during the approximately 30 min it took to mount the electrodes. The birds were allowed about 12 h to recover before they were permitted to dive. During that time they remained quiet in the corral and resting values of heart rate were obtained.

The pulmonary arterial catheterization procedure for cardiac output and stroke volume (V_s) measurements required intubation of the bird after the initial induction of anesthesia. After intubation with a 9 mm endotracheal tube, the bird was maintained at 1 % isoflurane and artificially ventilated with a tidal volume of 15 ml kg^{-1} at a rate of $15\text{--}20 \text{ min}^{-1}$. During anesthesia, rectal temperature was constantly monitored, and a core temperature of $38\text{--}39^\circ\text{C}$ was maintained by various surface cooling techniques such as snow or ice packs on feet and/or wings, a bed of snow below the body, and cooling of the hut. Anesthesia durations were about 2.5 h. Resting data were collected during the third and fourth hour after cessation of anesthesia. At such time, anesthetic gas concentrations are probably less than 90 % of the original anesthetizing concentration (Eger, 1974) and cardiovascular side effects should be minimal. At the conclusion of the measurements, the catheter was removed under general anesthesia, and the bird was returned to the outside corral.

Recorder

The recorder used in this study was a modification of one described elsewhere (Ponganis *et al.* 1990b). In brief, it was an 8086 microprocessor combined with an 8–32K memory chip. The unit was capable of recording eight different variables. The entire circuitry and batteries were embedded in electrical resin for water-proofing. The units were 15 cm long by 4 cm by 3 cm and weighed 350 g.

Cardiac output and stroke volume

Cardiac output was determined by thermodilution (Wessel *et al.* 1971). An Edwards pediatric (2 mm) Swan–Ganz catheter was introduced percutaneously into the internal jugular vein and passed to the pulmonary artery. Catheter position was confirmed by recognition of pulmonary artery pressure waveforms. For each measurement, 5 ml of iced saline was injected rapidly through the right atrial port of the catheter. The thermodilution curve was plotted with an Edwards Com-1 cardiac output computer, which also integrated the curve to give the output in l min^{-1} . Standard factory-supplied calibration constants were used in the calculations; factory specifications and clinical studies reveal such computations to be within $\pm 10\%$ of dye-dilution cardiac output determinations (Fischer *et al.* 1978; Runciman *et al.* 1981). Although such calculations assume a 5 % dextrose injectate, no correction was made for our use of saline as that substitution causes only a 2 % theoretical difference in results (Levett and Reploggle, 1979). Simultaneously, heart rate was obtained by counting the QRS complexes imaged on an oscilloscope. Both of these variables were determined at various times during anesthesia and for the first 5 h of recovery while the bird was resting quietly.

Heart rate

Heart rate was obtained by placing two copper wire electrodes subcutaneously along the midline of the back. They were held in place with 0 prolene suture and waterproofed with epoxy glue.

Resting values for heart rate were obtained over the 12 h recovery period, and dive values over the next 8–10 h while the bird dived and fed. The recorder detected the R wave, which was counted and logged every 15 s. At the same time, the microprocessor was recording depth every 4 s. The memory filled after about 5 h. Since the birds were exiting the water after every dive, it was easy to transfer the data to a laptop computer after a series of dives, clear the memory and start again.

In order to prevent any double counting of the R wave and the T wave, the microprocessor was programmed not to count a peak as an R wave unless the R–R interval was greater than a preprogrammed duration. This interval was set initially (1987) so that no heart rate values above $100 \text{ beats min}^{-1}$ could be counted. Some diving and surface recovery records were consistently above $100 \text{ beats min}^{-1}$ so that in 1988 this was raised to $120 \text{ beats min}^{-1}$. To confirm that what was being counted was the R wave only, a few records were obtained in two other ways. First, the microprocessor was programmed to record the electrical signal from the electrodes every 4 ms. This density of data points gave a profile of the QRST complex and confirmed that during the dive the recorder was accurately counting heart rates. In this configuration, the memory lasted for about 20 min of diving, which was adequate for this test.

Second, electrodes with quick releases were attached to the birds. Within about 60 s after they came to the surface, the quick release was plugged in and recovery heart rates were recorded with a portable, battery-powered oscilloscope. We found from these observations that within the first 2 min after surfacing the heart rates sometimes exceeded the $120 \text{ beats min}^{-1}$ maximum of the microprocessor (Fig. 2); therefore, the heart rates recorded by the microprocessor between dives may underestimate the initial surface rates. Because of this error, we have no statistical analysis or tabular presentation of between-dive heart rate data. The only such results are presented in one figure for illustrative purposes of the heart rate profile.

Swim speed

Speed was determined by means of a small paddlewheel coupled to either the multi-variable microprocessor, mentioned earlier, or most frequently to a unit dedicated to this task. This special microprocessor was 2 cm thick \times 4 cm wide \times 5 cm long and weighed 200 g. Every rotation of the wheel was counted and the velocity measured every 2 s (1988) or 15 s (1987). The paddlewheel had been previously calibrated on a submerged spindle in the ring tank at the Scripps laboratory as described by Ponganis *et al.* (1990b). The spindle was approximately the same mass and linear dimensions as an emperor penguin. The paddlewheel

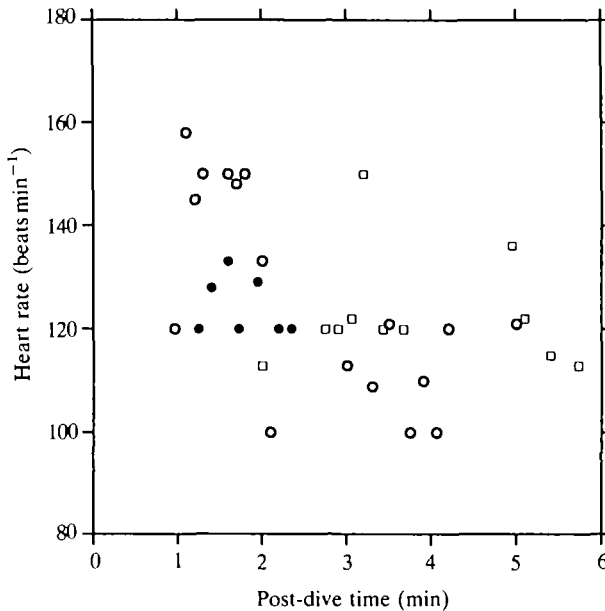


Fig. 2. Post-dive heart rates obtained from electrocardiogram tracings soon after the bird had surfaced from three different dives. ○, the rate following a dive that lasted 4 min 20 s, $N=17$; ●, the rate after a dive lasting 3 min 8 s, $N=7$; □, the rate after a dive lasting 4 min 50 s, $N=11$.

was mounted at the point of maximum diameter, which was in a similar position to where it was mounted on the penguins. Tests showed that if this varied by about 20% in a fore or aft position it had little effect on the results. The paddlewheel rotation speed was linear from 0.5 m s^{-1} to 3.4 m s^{-1} , the peak velocity of the test. The correlation coefficient of rotations to velocity was greater than 0.99.

Behavior of the birds while they swam within 60–100 m of the hole was observed from a sub-ice observation chamber that has been previously described in detail (Kooyman, 1968). The observer sits about 8 m below the surface and is surrounded by 6 rectangular view ports, each about $30 \text{ cm} \times 45 \text{ cm}$. From this vantage it was easy to observe the departure and arrival of the birds in water of more than 100 m visibility and note the response of the birds to the pack, their swim speed between two holes about 30 m apart, and the effort of the encumbered bird.

There was no observable response of the birds to the microprocessor pack, either on the surface or while diving. Since the birds always swam together, it was used as a gauge for the level of encumbrance of the recorder. Encumbered birds departed with the other birds but usually returned last, but still as part of the group. Therefore, their swim speeds are an accurate measure of the birds during these types of shallow feeding dives. However, the swim effort for the instrumented bird was greater, and they compensated not so much by lagging behind the other birds but by occasionally skipping dives with the group.

Data transfer and analysis

Data were transferred from the microprocessor to a personal computer and stored on diskettes for further analysis. Initial data review utilized a customized Pascal analysis program. Microprocessor data were imported directly into Quattro Pro for arithmetic and graphic analysis. Statistical tests utilized the Statistix statistical package.

Results

Eleven birds were studied in the austral summer of 1987–1988, 1988–1989 and 1989–1990. The basic information on each bird and the experiments in which they participated are summarized in Table 1. All gained weight during their captivity and all had enough specific behavioral and physical traits for them to be identified without relying on the feather-clipped marks.

Cardiac output and stroke volume

Cardiac output and Vs were obtained in two birds 3–4 h after anesthesia while the birds stood in a transport box. These results are summarized in Table 2. Penguin 2-89 slept almost constantly during the study period. Penguin 6-88, in contrast, was primarily awake during the study period and cardiac output and Vs were greater than those of 2-89, but heart rate was lower (Student's *t*-test, $P=0.19$ for heart rate, $P<0.0001$ for cardiac output and Vs).

*Heart rate**Resting*

The resting heart rates are summarized in Table 3. The overnight resting values are high for about the first hour and then rise again about an hour before the end of the night. These are excitatory phases following and preceding our handling of the birds. Four plots illustrating this pattern are presented in Fig. 3. The excitatory periods were eliminated from the calculation of the resting means. The resting means range from 56 to 80 beats min⁻¹.

Table 2. *Emperor penguin cardiac outputs and stroke volumes*

	Bird no. 6-88			Bird no. 2-89		
	Cardiac output (ml kg ⁻¹ s ⁻¹)	Heart rate (beats min ⁻¹)	Stroke volume (ml kg ⁻¹)	Cardiac output (ml kg ⁻¹ s ⁻¹)	Heart rate (beats min ⁻¹)	Stroke volume (ml kg ⁻¹)
Mean	2.86	64	2.7	1.87	71	1.6
S.D.	1.12	22.93	0.77	0.53	19.06	0.31
N	34	34	34	47	47	47
Maximum	5.82	139	5.1	3.42	115	2.5
Minimum	1.43	27	1.5	1.08	46	1.1

Data were recorded during the third and fourth hours after the end of anesthesia.

Table 3. *Summary of overnight resting heart rates, sampled every 16 s*

Bird number	Mean (beats min ⁻¹)	±s.d.	N
1-87	80	5.4	3668
2-87	56	12.1	2759
3-87	70	10.4	2139
1-88	77	14.8	2769
1-88	71	11.9	1812
9-88	77	8.1	1435
Average of means	72		

The analysis was made on those samples taken before and after the active phases that followed and preceded handling.

s.d. is one standard of the mean and *N* is the sample size.

Diving

Diving heart rates are summarized in Table 4, which also includes the statistics for depth and velocities that were measured concurrently. The diving heart rates are significantly different from resting rates in three individuals: 3-87, 1-88 and 9-88 (for each *t*-test, $P < 0.001$). In some instances during 1987, the birds were chased by Weddell seals. These values are indicated in Table 4, and they tended to be higher than when no seals were nearby. Especially noteworthy are 2-87 and 3-87. Heart rates were obtained from 3-87 under both conditions, and the rates when seals were present were significantly higher (*t*-test, $P < 0.001$). This is illustrated in the extreme for 2-87 where heart rates were *higher* during swim periods than when

Table 4. *Summary of average diving heart rate, depth and velocity, all of which were recorded concurrently*

Bird number	Heart rate (beats min ⁻¹)	Maximum depth (m)	Swimming speed (m s ⁻¹)
1-87	63 (21.6, 419)	19 (11.8, 23)	2.8 (1.12, 248)
2-87*		41 (19.5, 26)	3.4 (1.03, 703)
3-87	65 (30.5, 387)	37 (9.5, 21)	2.4 (0.77, 347)
3-87*	100 (19.3, 213)	29 (8.0, 11)	2.5 (1.11, 213)
1-88	65 (20.4, 161)	28 (14.7, 7)	
9-88	60 (18.2, 238)	25 (14.5, 16)	
Average of means (not including 2-87* and 3-87*)	63.3		2.8

Values in parentheses are ±one standard deviation and sample size.

Values from birds harrassed by seals are indicated with an asterisk.

Sample rate was every 16 s.

There are no heart rate values for 2-87 because the rate exceeded the counting limit of the recorder so frequently.

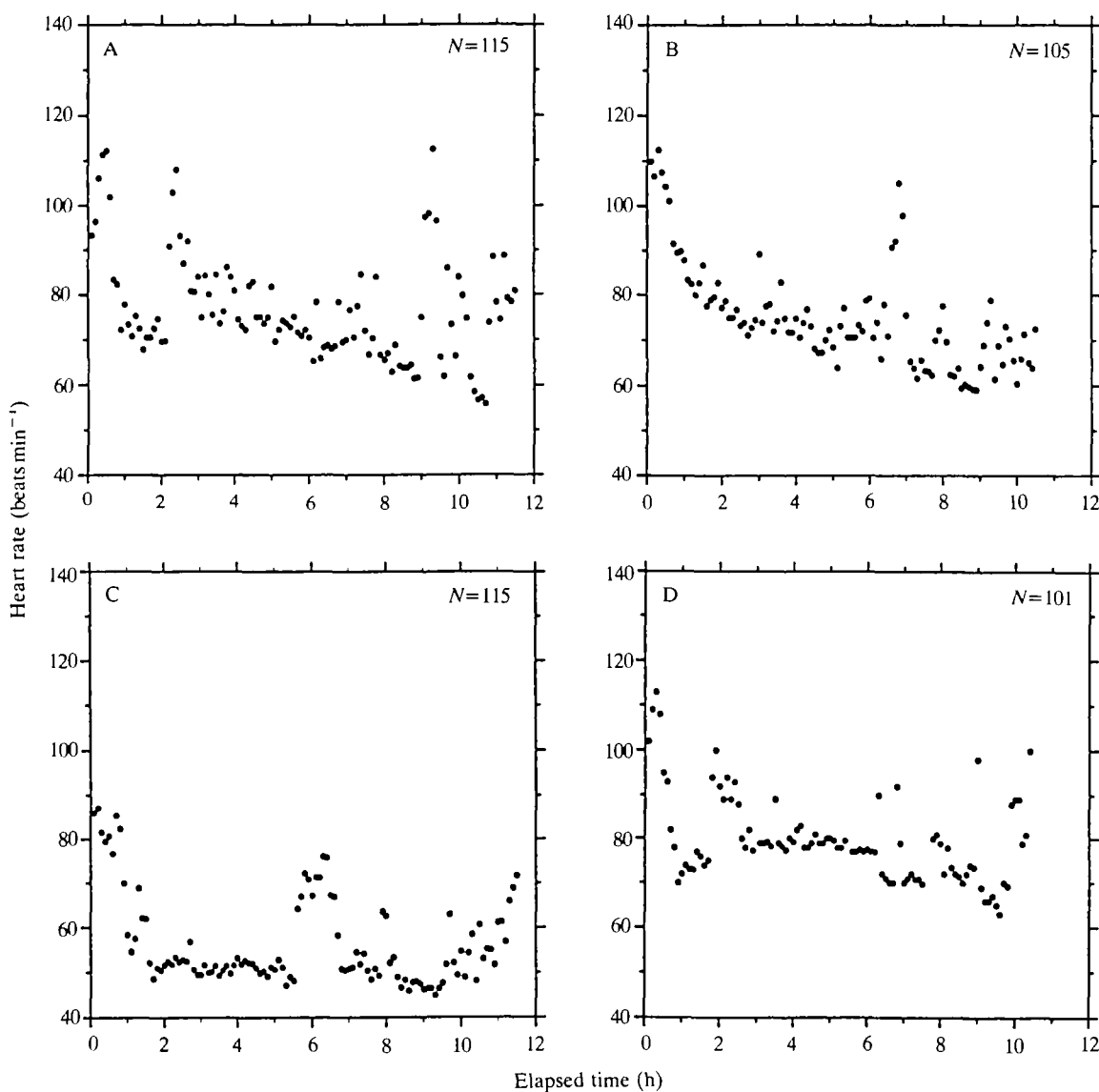


Fig. 3. Pattern of change in overnight resting heart rate; the N values are 10 min averages of the samples taken every 16 s. (A) 1-88 during the first night; the start time was 21:00 h; (B) 1-88 during the second night; the start time was 22:00 h; (C) 2-87 start time was 23:00 h; (D) 9-88 start time was 23:00 h.

on the surface. Swim speeds were also high at about 4 m s^{-1} (Fig. 4A). This was not a typical dive bout, and there were probably numerous brief surfacings that were too rapid for the microprocessor to detect and in which the birds never stopped swimming.

1-87, to our knowledge, was not chased by any seals. The heart rates declined

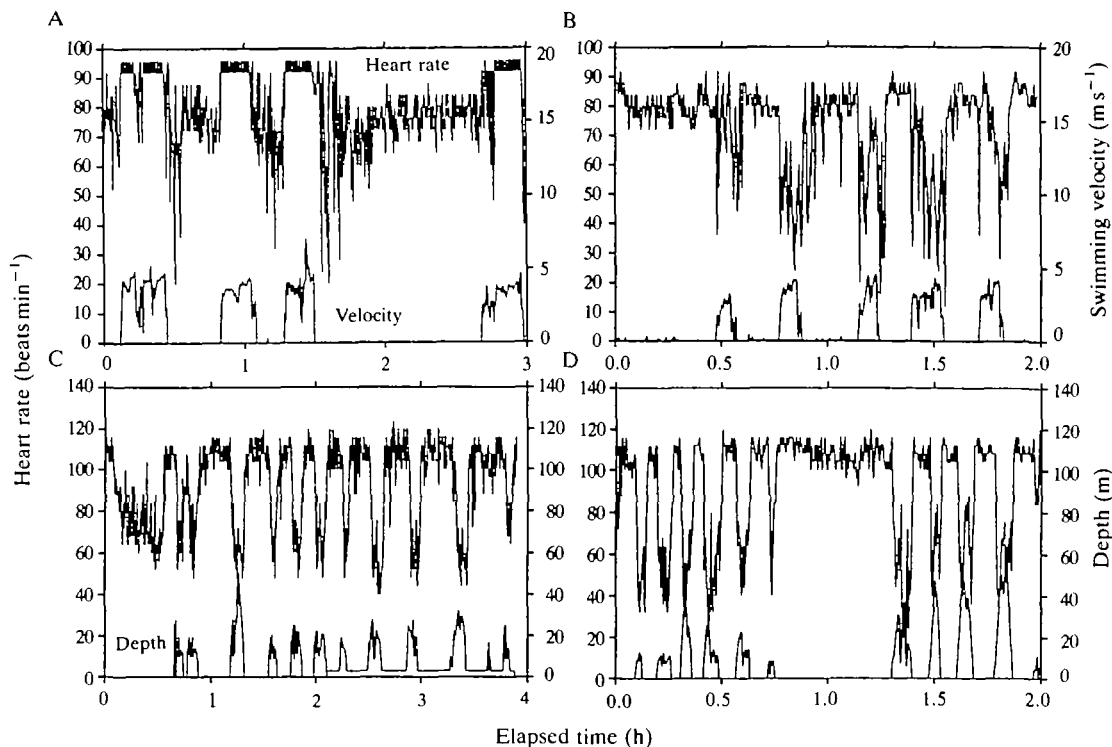


Fig. 4. Patterns of diving heart rates (upper traces) in emperor penguins. (A) 2-87 diving heart rate for five dives. Surface intervals were too brief for the microprocessor to detect, so that apparent dives may include more than one dive; (B) 1-87 diving heart rate for five dives. The diving duration ranged from 4.7 to 6.8 min. (C) 1-88 diving heart rates for 12 dives that ranged in duration from 3 to 7 min; (D) 9-88 diving heart rates for 11 dives that ranged in duration from 2 to 6 min. Note that the abscissa scale is not the same for all plots.

but they were more erratic than in 1-88 and 9-88 (Fig. 4B). The dives of 1-88 can be distinguished easily by the abrupt drop in heart rate, which fell from a pre-dive value of about $105 \text{ beats min}^{-1}$ to about $60 \text{ beats min}^{-1}$ (Fig. 4C). In this plot, an initial excitatory phase (post-handling) can be seen after which, in the course of the 40 min before the first dive, the rate falls to the normal level of about $65 \text{ beats min}^{-1}$ before rising sharply a few minutes before the dive. 9-88 shows a similar pattern to 1-88 except that the dive heart rates tend to drop to a lower rate of $55 \text{ beats min}^{-1}$ (Fig. 4D and Table 4).

There appeared to be no relationship between heart rate and speed. There was also little correlation between heart rate and dive duration in two birds (Fig. 5) in which the correlation coefficients (r) were 0.17 for 9-88 and 0.36 for 1-88.

An example of heart rates during an exceptionally long dive is shown in Fig. 6. In this dive lasting nearly 10 min of 1-88, the rate declines to about $30 \text{ beats min}^{-1}$ from the surface rate of about $110 \text{ beats min}^{-1}$. The rate remained low until about

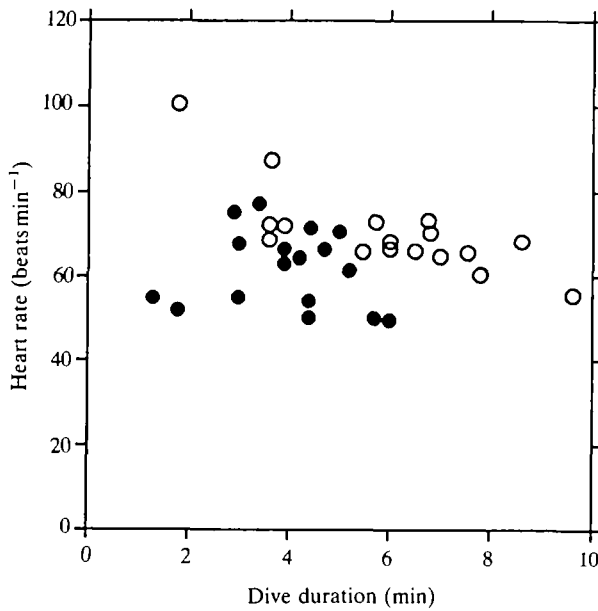


Fig. 5. Heart rate in relation to dive duration for 1-88 (○) and 9-88 (●). Each point is the average for the heart rate measured at the indicated time interval. The regression equations for 1-88 and 9-88 are: d.f.=198, $y=90.9-3.68x$, $r=0.36$ and d.f.=414, $y=72.5-3.01x$, $r=0.17$, respectively. d.f. is degrees of freedom.

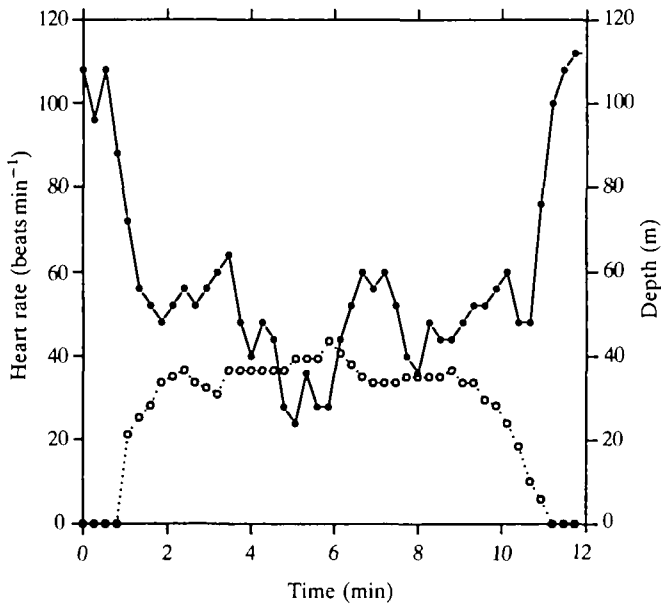


Fig. 6. Heart rate (●) and depth profile (○) during a 10 min dive by 1-88.

1 min before the end of the dive, when it steadily increased to the between-dive tachycardia.

Interdive

In 1987, surface heart rates were often lower than diving heart rates. As previously discussed, high heart rates were often seen during diving, especially when seals were present. In addition, in that year the birds often rapidly surfaced, breathed and dived again without leaving the water. Although documented by visual observations at the surface and from the sub-ice observation chamber, such short dives were not distinguishable on the microprocessor record. Some of the high heart rates in the 1987 dives may be due to tachycardia associated with eupnea at the surface. Heart rates recorded by the microprocessor during interdive surface intervals are, at times, underestimates. Heart rates above $120 \text{ beats min}^{-1}$ could not be recorded because of the microprocessor's programmed refractory period. As seen in Fig. 4, interdive surface heart rates were in the range of $100\text{--}120 \text{ beats min}^{-1}$ in 1-88 and 9-88. Higher rates probably occurred. In 9-88, the microprocessor was programmed to record the electrocardiogram (EKG) complex continuously in one 20 min sampling. Manual calculation of the heart rate (in 15-s intervals) from the printout revealed mean interdive surface rates between 158 and $188 \text{ beats min}^{-1}$ over 3–11 min of surface time. The maximum was $228 \text{ beats min}^{-1}$; the minimum was $104 \text{ beats min}^{-1}$. These data are higher than the post-dive heart rates obtained from 2-88 oscilloscope EKG tracings (Fig. 2), which suggests a high degree of variability, either between birds or as a result of behavior during and after the dive.

Speed

Swim speeds are summarized in Table 5. The overall average of the means is

Table 5. *Summary of average swimming speeds recorded with the velocity meter only for 1988 and with the velocity and heart rate recorders for 1987*

Bird number	Speed (m s^{-1})	S.D.	Sample size	Maximum speed (m s^{-1})	Sample interval (s)
1-87	2.7	1.16	253	4.6	16
2-87	3.4	1.07	703	7.1	16
3-87	2.4	0.77	352	5.6	16
2-88	3.3	0.76	257	4.5	2
2-88	2.8	0.98	77	4.2	8
3-88	3.6	0.67	1524	5.9	2
4-88	2.4	1.04	332	4.6	2
8-88	2.5	1.13	1247	5.5	2
9-88	3.6	0.85	492	4.9	2
9-88	3.1	0.64	444	5.6	8
Average of means	2.98				

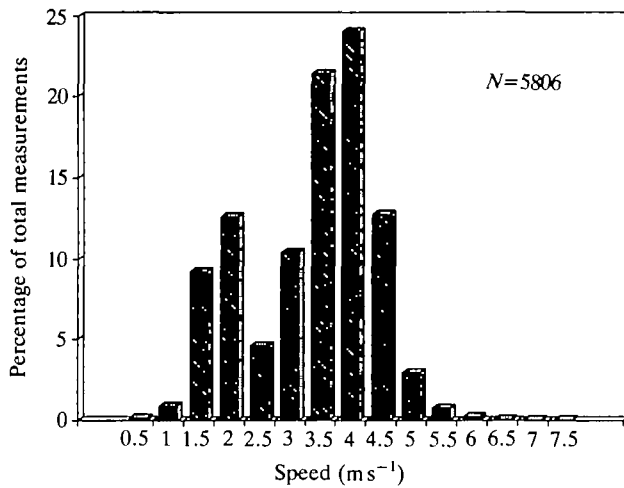


Fig. 7. Frequency distribution of swimming velocities for birds 1-87, 2-87, 3-87, 2-88, 3-88, 4-88, 8-88 and 9-88 that were summarized in Table 5.

2.98 m s^{-1} from 10 separate sampling periods. The maximum speed obtained for each bird ranged from 4.6 to 7.1 m s^{-1} , from a total sample size of 5681. The various sample intervals of 1.86 – 16 s did not seem to influence the maximum or average speeds obtained. An analysis of frequency of occurrence of speeds summed in 0.5 m s^{-1} intervals showed that the distribution is skewed towards the high speeds, with an abrupt decline above 4.5 m s^{-1} ; the mode is 4 m s^{-1} , the median is 3.3 m s^{-1} and the mean is 2.98 m s^{-1} (Fig. 7).

Finally, some swim speeds were obtained directly from the observation chamber as the birds swam a known distance when departing from the hole. The mean rate of $2.5 \pm 0.86 \text{ m s}^{-1}$ ($N=13$) is lower than that measured with the velocity meters, as is the maximum speed observed of 3.8 m s^{-1} . These results are expected since the birds were usually descending, probably at a lower speed while they overcame positive buoyancy. Also, the maximum speed is taken from a much smaller sample size than those obtained from the microprocessor.

Discussion

Cardiac output and stroke volume

Cardiac output and V_s were obtained simultaneously only when the birds were resting (Table 2). These values were determined primarily during apnea and mixed apnea–eupnea periods. The duration of eupnea and its associated tachycardia was too short to allow exclusive eupneic cardiac output determinations. The cardiac output and V_s data are those of a bird standing in a confined space. Cardiac output and V_s were greater in the awake bird. These differences may be due to individual variation or to differences in venous return during awake and sleeping states. Nevertheless, these data establish in the emperor penguin an

average resting cardiac output range of $1.9\text{--}2.9\text{ ml kg}^{-1}\text{ s}^{-1}$ and V_s of $1.6\text{--}2.7\text{ ml kg}^{-1}$. We know of no other values for resting birds of comparable size. Compared to dogs and goats of 28.8 and 30 kg, respectively, the cardiac output and V_s are similar. In dogs and goats standing at rest, cardiac outputs are 2.6 and $3.1\text{ ml kg}^{-1}\text{ s}^{-1}$, respectively, and the V_s stroke values are 1.9 and 2.2 ml kg^{-1} , respectively (Karas *et al.* 1987). Seals and sea lions of 31–38 kg also have values similar to these. Seals, which are arrhythmic breathers, have an apneustic pause between breathing cycles. This results in a cardiac output range from $4.4\text{ ml kg}^{-1}\text{ s}^{-1}$ while breathing to $2.3\text{ ml kg}^{-1}\text{ s}^{-1}$ while breath-holding (Ponganis *et al.* 1990a). Since breath-holding in seals dominates most of the time, it might be assumed to be the normal resting level. In contrast to the measured V_s of other resting mammals, the V_s of harbor seals also changes during apneusis and ranges from 2.9 ml kg^{-1} in eupnea to 1.9 ml kg^{-1} in apnea. In sea lions, the cardiac output is $2.7\text{ ml kg}^{-1}\text{ s}^{-1}$ and the V_s is 2.1 ml kg^{-1} (Ponganis *et al.* 1991). In this species there was no obvious arrhythmic breathing during these measurements, although such arrhythmias were noted by Lin *et al.* (1972) during some studies of heart rate.

Heart rate

Resting

The overall average heart rate of the penguins was 72 beats min^{-1} (Table 3). This is lower than that of dogs and goats, 82 and 86 beats min^{-1} , respectively, standing quietly (Karas *et al.* 1987). However, the birds at times were lying down and sleeping so the differences are probably more due to the conditions of measurement. In the harbor seals mentioned earlier, the heart rates ranged from 50 to $120\text{ beats min}^{-1}$ during apnea and eupnea. The resting rate of sea lions of a mass of $40\text{--}50\text{ kg}$ and while lightly restrained ranged from 85 to $114\text{ beats min}^{-1}$ (Lin *et al.* 1972). According to the authors, the more normal condition was the rate while in apnea.

The only other penguin species for which we know of resting heart rates under unrestrained conditions is the small (4.5 kg) Humboldt penguin. In these captive birds, their resting heart rate ranged from $121\text{ beats min}^{-1}$ on land to $139\text{ beats min}^{-1}$ when floating on water (Butler and Woakes, 1984). We have no comparable heart rate while resting in water for emperors because they only rested on the ice.

Diving

There are no measurements of unrestrained diving heart rates for a bird or mammal of similar size. In fact, the only other diving tetrapod for which there are similar data when diving under natural conditions is the Weddell seal. In this seal of $350\text{--}450\text{ kg}$, the heart rates, whilst resting or sleeping on ice and breathing and breath-holding, are $55\text{--}45\text{ beats min}^{-1}$ (Kooyman, 1968). The rate declines to about 30 beats min^{-1} during normal diving durations and may drop as low as 16 beats min^{-1} during extended dives (Kooyman and Campbell, 1973; Hill *et al.* 1987).

If one assumes that the resting apnoea of $45 \text{ beats min}^{-1}$ while sleeping on ice is the normal maintenance value for Weddell seals, then the decline during diving ranges from 33 % to a maximum of 64 %. This rate supports the needs of the seal while it is swimming at about 2 m s^{-1} (M. A. Castellini, in preparation). The overall heart rate while diving in emperor penguins is $63 \text{ beats min}^{-1}$ (Table 4) which is about 15 % lower than resting values, a lesser decline to that in the Weddell seal. This rate excludes those instances where seals were present under the ice, which caused some excitement in the birds.

There are only two other studies where heart rate was measured in freely diving penguins, although they were in rather unnatural conditions. In a study of the much smaller gentoo penguin swimming near shore and on a tether, heart rates appeared to decline to about $75 \text{ beats min}^{-1}$ during dives and rise to $180 \text{ beats min}^{-1}$ while on the surface (Millard *et al.* 1973). In the other investigation (Butler and Woakes, 1984), Humboldt penguins were diving in a small, shallow pool. No swim speeds were reported, but they were probably low because of the pool size. Under these conditions, the diving heart rate was about the same as that when the birds were resting in water and higher than when they were resting on land. This study contrasts with the emperor penguin. An important difference in behavior was in the diving duration. In the Humboldt penguin, the duration of the dives was short. The maximum was about 60 s, but in the emperor penguin all dives exceeded 1 min, most were about 3–4 min in duration and exceptional dives lasted 10 min.

In the 10 min dive illustrated in detail in Fig. 6, the heart rate declined soon after diving and reached a level as low as $30 \text{ beats min}^{-1}$, 50 % less than the overnight resting mean. This is lower than the average diving heart rate of all birds studied, and the average for the dive was about 10–15 % lower than the overall average of diving means (Table 4). However, there was no correlation between heart rate and diving durations ranging from 1 to 10 min (Fig. 5). No analysis of correlation of heart rate to depth was made because of the narrow depth range to which the birds dived in comparison with their foraging depth range.

Speed

The frequency distribution analysis shows the most common speeds to be between 3 and 4 m s^{-1} (Fig. 7). It should be noted that the maximum calibration speed was 3.6 m s^{-1} . We assume that the paddlewheel continues to respond linearly at the higher speeds measured. The assumption seems reasonable, based on the linearity of the calibration curve and the histogram analysis. With the exception of speed just above the maximum calibration speed (3.5 – 4.0 m s^{-1}), there was a marked decline in frequency of speed measurements higher than the calibration to contribute an error to the frequency distribution assessment.

It seems that the overall average mean speed of emperor penguins of nearly 3 m s^{-1} (Table 5) is exceptionally high for diving vertebrates. Using these same recorders and under the same experimental conditions, we obtained swim rates from Weddell seals that were just under 2 m s^{-1} (M. A. Castellini, in preparation).

Also, the same types of recorder were used on sea lions and fur seals, where swim speeds averaged about 1.5 ms^{-1} (Ponganis *et al.* 1990b), or half that of the emperors.

The emperor swim speeds are also higher than those obtained for other penguins. The overall average speed for king penguins on foraging trips is $2.2\text{--}2.4 \text{ ms}^{-1}$ (Adams, 1987; Kooyman *et al.* 1991). In three other species of antarctic penguins – Adélie, chinstrap and gentoo – they averaged about 2.2 ms^{-1} (Wilson *et al.* 1989). Speeds for the smallest of all penguins, the little blue penguin, averaged 2.4 ms^{-1} (Gales *et al.* 1990). The jackass penguin averaged 1.8 ms^{-1} (Nagy *et al.* 1984). In short, based on our measurements, the emperor may swim about 40–50 % faster than other penguins. However, our measurements were obtained from sampling intervals of 2–16 s. The little blue penguin measurements were also taken at brief intervals of every 9 s. All the other speeds of penguins were the preferred or roughly the modal value for an entire foraging cycle, which may have been several hours to several days long.

Diving response and oxygen management

If we assume that the V_s remains constant when heart rate changes, then cardiac output drops about 13 % during unstressed dives. However, propulsive muscle activity has increased from rest to contraction rates matching a wingbeat frequency of about 40 min^{-1} , at least in the early part of the dive while we could observe birds descending from the dive hole. Since muscle requirements in mammals at rest demand about 15 % of cardiac output (Astrand and Rodahl, 1977), we speculate that this drop in cardiac output is due primarily to the elimination of blood flow to muscle, despite the fact that muscle energy demands have increased several-fold. If this is the case, then propulsive muscles are without blood flow during the dive and rely on their internal O_2 stores for aerobic metabolism. The muscle O_2 stores of emperor penguins are large, but not exceptional compared to those of other divers (Kooyman, 1989). Certainly for the length of many of the dives observed in this study, and of common foraging diving durations noted in other studies under more natural conditions (G. L. Kooyman, unpublished observations), the O_2 store ought to become exhausted if oxygen depletion rate approximates that measured by Scholander (1940).

Scholander found in the gentoo penguin, the only measurement of muscle O_2 content ever made in a breath-holding bird, that the content fell to zero within 5 min after forced submersion began. If the emperor penguin follows a similar pattern, then the bird must rely on anaerobic metabolism during some dives; perhaps any lasting longer than 5 min.

According to their muscle chemistry and morphology, this species is poised for such an energy production pattern (Baldwin, 1988). This contrasts with the observation and conclusions for Humboldt penguins (Butler and Woakes, 1984), and also with the observations for Weddell seals (Kooyman *et al.* 1980, 1983) and with calculated aerobic dive limits (ADL) for fur seals and sea lions (Gentry *et al.* 1986) as well as for other diving vertebrates (Kooyman, 1989). However, the

observations agree with calculations and predictions for king penguins, in which it has been estimated that 40 % of their foraging dives exceed their hypothetical ADL (Kooyman *et al.* 1991). If emperor penguins exceed their hypothetical ADL regularly, this indicates important physiological, morphological and behavioral differences related to diving between penguins and seals. Either the mammal-based ADL theory is not applicable to king and emperor penguins or the birds may be routinely diving well beyond their expected ADL. In conclusion, it appears that emperor penguins and mammals of similar body mass have similar resting heart rates, cardiac outputs and stroke volumes. Furthermore, emperor penguins and Weddell seals may have an equivalent magnitude of heart rate decline during diving. Nevertheless, despite these basically similar cardiovascular variables, the birds manage to swim faster while diving.

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