

Reports

Diving Depths and Energy Requirements of King Penguins

Abstract. During 4- to 8-day periods at sea, half of 2595 dives of three king penguins were more than 50 meters and two dives exceeded 240 meters. The at-sea metabolic rate, estimated from the turnover of tritiated water, was 2.8 times the standard metabolic rate and requires about 2.5 kilograms of squid per day. Ten percent or less of the dives may result in prey capture.

A small number of diving depths have been directly measured in emperor penguins (*Aptenodytes forsteri*) (1). As far as we know, all other investigations of the diving depths of aquatic birds have relied on circumstantial evidence such as the type of food captured and the depths at which birds were trapped in nets (2).

Using a recently developed depth recorder (3), we measured the diving depths of three king penguins (*Aptenodytes patagonica*). The birds' depths frequently exceeded 100 m, but the penguins rarely dived deeper than 240 m. By

measuring the tritiated water turnover (4), we estimated the energetic requirements of foraging in three other birds as two to three times more than that of the standard metabolic rate (SMR). On the basis of the estimated masses of squid consumed, only about 10 percent of the dives would have resulted in prey capture.

We captured six adult king penguins, each weighing 12 to 14 kg, near their breeding colony at Schlieper Bay, South Georgia Island in February 1980. The birds were captured just before they

went to sea to collect food for their chicks. Depth histogram recorders (DHR) (3) were clamped to the feathers between the scapulae of three of these birds (P1, P2, and P3), and then the birds were released immediately. Three other birds (P4, P5, and P6) were weighed, individually marked, and injected with 0.3 mCi of tritiated water (HTO) into the brachial vein. These birds were held for 1.5 hours while the HTO equilibrated with total body water. Just before release, a 10-ml blood sample was taken from the brachial vein. When the birds returned 4 to 8 days later, they were reweighed and a second 10-ml blood sample was taken as before. The blood samples were stored for later analysis of HTO changes and estimates of water turnover (5).

During a total of 18 days at sea (4 to 8 days per bird), 2595 dives were recorded for three penguins. The birds averaged 144 dives per day. The frequency analysis of these diving depths is shown in Fig. 1. The most frequently logged depth range was 5 to 50 m. If the minimum threshold of the recorder on P2 (35 m) had been as low as that of P1 and P3 (5 m), the P2 recorder would have logged probably another 400 dives. The majority of the dives of P1 and P3 in the 5- to 50-m range were less than 35 m. There were 1304 dives (50 percent) that exceeded 50 m. There was an almost linear decline in the number of dives in each grouping up to the last range of 241 to 290 m, which included only two dives.

Shallow dives (< 30 m) are difficult to interpret because it takes little effort for the penguins to reach such depths. On the other hand, dives in excess of 50 m require a serious swimming effort by the penguins and we therefore interpret them as foraging dives.

The large number of deep dives indicates that king penguins frequently, if not predominantly, feed deeper than other South Georgia birds (6). Furthermore, the deepest dives (> 240 m) are considerably deeper than has been recorded for any aquatic bird except the king penguin's near relative, the emperor penguin, which dives to at least 265 m (1).

Total body water, as determined by the method of Foy and Schneider (7), represented 60 percent of the body mass. The average water turnover at sea was 2.2 liters per day or 29 percent of the body water pool (Table 1). The various assumptions involved in the measurement of water flux in free-ranging animals (8) either were valid for our determinations or were considered as not introducing serious errors. Therefore, using the method of Shoemaker *et al.* (4),

Table 1. Water turnover and estimates of metabolism and food consumption at sea for three king penguins. The standard metabolic rate (SMR) was estimated from the equation of Aschoff and Pohl (10) for nonpasserine birds: $SMR = 4.41 B^{0.729}$, where SMR is in watts and B is the body mass in kilograms; ww = wet weight.

Bird	Body mass (kg)	Total body water (liters)	Days at sea	Water turnover at sea (liter day ⁻¹)	Squid consumed per day at sea [kg (ww) day ⁻¹]	Metabolic rate at sea (W kg ⁻¹)	Total energy expended at sea (kJ kg ⁻¹ × 10 ³)	Metabolic rate at sea/SMR
P4	12.2	7.5	4	2.0	2.3	6.1	2.1	2.7
P5	13.2	8.0	5	1.5	1.7	4.2	1.8	1.9
P6	13.7	7.8	2	3.0	3.5	8.1	1.4	3.7
Mean	13.0	7.8	3.7	2.2	2.5	6.1	1.8	2.8

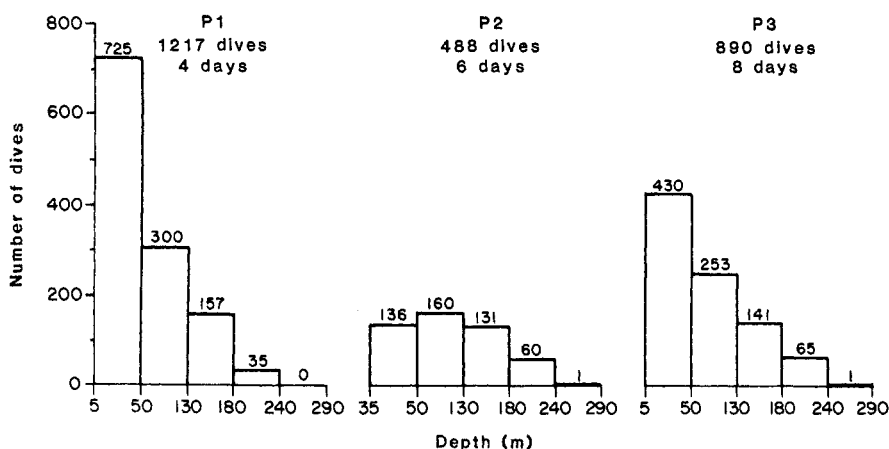


Fig. 1. Frequency analysis of the diving depths of three king penguins. All three birds departed and returned to the Schlieper Bay colony within 4 to 8 days. The minimum threshold of the depth recorder for P2 was higher than for the other two penguins.

we calculated an average daily metabolic rate (ADMR) at sea of 6.1 W kg^{-1} (Table 1).

The metabolic rate for a 13-kg penguin tending a chick is 4.3 W kg^{-1} ; this rate is based on a mean weight loss of 0.15 kg day^{-1} (9). The ADMR at sea was about 1.5 to 2 times the ADMR of birds on the rookery. Since the SMR of a resting nonpasserine bird is 2.2 W kg^{-1} (10), our value of ADMR at sea is in good agreement with a value of two to three times the SMR determined for foraging terrestrial birds and mammals (11).

In comparing effort and success among the birds, we see that P5 expended half as much energy per time as P6, but it stayed at sea over twice as long. Overall, its total expenditure was average (Table 1). The dive data (Fig. 1) also show similar disparities of effort in that P1 made 1217 dives in 4 days (304 dives per day), and P3 made 890 dives in 8 days (111 dives per day). It would seem that at times birds go to sea for less time but work harder.

The three tritiated birds expended from 19×10^3 to $26 \times 10^3 \text{ kJ}$ of energy while at sea. This corresponds to the consumption of a total of 7 to 9 kg of squid (12). In February, an 8-kg chick is fed about every 4 days and it gets about 3 kg of squid per visit (9). Thus the energy cost of foraging is over twice as great as the energy content of the food delivered to the chick. Measurements of their beaks suggest that the squid taken probably weigh about 150 to 200 g. Therefore, during one trip, some 50 to 90 squid need to be caught to sustain the adult and feed the chick. With an average of 865 dives per bird per trip, a king penguin is likely to make a catch on fewer than 10 percent of the dives.

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References and Notes

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3. The depth recorder used was 2.3 cm in diameter and 9.5 cm long and had a mass of 95 g. The unit consisted of a series of eight electronic counters, each set at a different threshold. Pressure was converted and linearly related to a voltage shift with an Entran pressure transducer. If the voltage exceeded the threshold of the counter, it was stored. When the recorder was recovered, the number of dives logged in each counter was

determined and a frequency analysis of the number of dives within the given depth ranges was the result [G. L. Kooyman, J. O. Billups, W. D. Farwell, in *Experimental Biology at Sea*, A. G. MacAlister and I. G. Priede, Eds. (Academic Press, New York, in press)].

4. V. H. Shoemaker, K. A. Nagy, W. R. Costa, *Physiol. Zool.* **49**, 364 (1976). The equation for calculating feeding rate from water turnover is

$$r_F = \frac{r_w}{P_w + E_F E_m M_w}$$

where r_F is the number of grams of dry food (F) consumed per kilogram of body weight per day, r_w is the total water turnover in milliliters per kilogram per day, P_w is the amount of preformed water per gram of F ($= 4.0 \text{ ml per gram of F}$), E_F is the number of kilojoules of energy per gram of F ($= 17.6 \text{ kJ per gram of F}$), E_m is the number of kilojoules metabolized per kilojoule of F ingested, and M_w is the water produced per kilojoule of F metabolized. The feeding rate (r_F) is converted to energy metabolized (in watts per kilogram) by

$$\text{ADMR} = r_F E_F E_m k$$

where k is a constant that converts the units to watts per kilogram ($k = 1.157 \times 10^{-8} \text{ W day}^{-1} \text{ kJ}^{-1}$). The food is assumed to be squid, the composition of which was obtained from B. R. Watt and A. L. Merrill [Composition of Food (Agriculture Handbook No. 8, Department of Agriculture, Washington, D.C., 1963)]. The value of M_w ($= 0.12 \text{ ml of water per kilocalorie of F metabolized}$) was calculated from the water produced from the oxidation of fat, carbohydrate, and protein [K. Schmidt-Nielsen, *Animal Physiology* (Cambridge Univ. Press, Cambridge, 1979)]. The value of E_m ($= 0.80 \text{ kcal metabolized per kilocalorie of F ingested}$) was based on energy assimilation measurements of Adélie penguin chicks (*Pygoscelis adeliae*) as determined by D. P. Costa (unpublished data) and for other marine birds by E. H. Dunn (*Condor* **77**, 431 (1975)) and J. A. Kushlan [*ibid.* **79**, 31 (1977)].

5. K. A. Nagy, V. H. Shoemaker, W. R. Costa, *Physiol. Zool.* **49**, 351 (1976).
6. J. P. Croxall and P. A. Prince, *Biol. J. Linn. Soc.* **14**, 103 (1980).

7. J. M. Foy and H. Schneider, *J. Physiol. (London)* **154**, 169 (1960).
8. K. A. Nagy and D. P. Costa, *Am. J. Physiol.* **238**, R454 (1980), equation 1. The assumptions are as follows: (i) body water is constant, (ii) water turnover is constant, (iii) the isotope labels only the body water, (iv) the isotope is lost only in the form of water, (v) there is no selective loss of tritium or unlabeled water, and (vi) there is no water input by way of the skin or lungs or by drinking. In calculating the free-ranging metabolic rates at sea, two of these assumptions may introduce significant errors. We assumed that the water influx consisted solely of preformed water in a diet of squid and water produced from oxidative metabolism. If the penguins drank seawater, the calculated metabolic rates are too high and therefore represent the maximum possible values. We also assumed that the birds were in energy balance during this part of the reproductive cycle. Since body weights changed less than 4 percent while at sea, this assumption, if wrong, would introduce only a small error.
9. B. Stonehouse, *Br. Antarct. Surv. Sci. Rep.* **23** (1960); J. P. Croxall, *J. Anim. Ecol.* **51**, 177 (1982).
10. J. Aschoff and H. Pohl, *J. Ornithol.* **111**, 38 (1970).
11. J. A. Gessaman, in *Ecological Energetics of Homeotherms* (Monograph Series, vol. 20, Utah State Univ. Press, Logan, 1973), p. 3.
12. The average energy content of squid is 3.48 kJ g^{-1} , and the assimilation efficiency is 80 percent [J. P. Croxall and P. A. Prince, *Br. Antarct. Surv. Bull.* **55**, 27 (1982)].
13. This work was supported by National Science Foundation grant DPP 78-22999 and National Institutes of Health postdoctoral fellowship PHS AM06093-01 to D.P.C. Logistic support was provided by the staff of the British Antarctic Survey to whom we are most grateful, particularly R. D. Bell and D. W. Doig, who provided assistance in the field. D. M. Boone and W. Farwell gave considerable effort to final troubleshooting and making ready the DHR's. We appreciate K. A. Nagy's review of an early draft of the report.

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Hypotensive Effect of Fasting: Possible Involvement of the Sympathetic Nervous System and Endogenous Opiates

Abstract. Fasting lowers blood pressure to a greater extent in spontaneously hypertensive rats than in normotensive rats. While fasting reduced cardiac sympathetic activity to an equivalent extent in both groups of animals, only in the hypertensive rats did fasting elicit an opiate-mediated vasodepressor response that was independent of sympathetic withdrawal. Both sympathetic nervous system suppression and endogenous opiate activation, therefore, may contribute to the hypotensive effect of fasting in the spontaneously hypertensive rat.

The hypotensive effect of fasting or caloric restriction is greater in hypertensive subjects than in normotensive subjects (1-4). In a recent study 4 days of fasting reduced systolic blood pressure 19 percent in spontaneously hypertensive (SH) rats and only 7 percent in the related normotensive Wistar-Kyoto (WKY) strain (3). Although numerous hypotheses have been suggested to account for this hypotensive response to fasting, none has gained general acceptance (1-4). The observation that fasting suppresses sympathetic nervous system (SNS) activity (5) has raised the possibility that the sympatholytic effect might contribute to the fall in blood pressure. We report here studies to assess the role of diminished SNS activity in fasting-

induced blood pressure decreases in SH and WKY rats.

The effect of fasting on the turnover of tritiated norepinephrine in cardiac tissue (6) was measured simultaneously in SH and WKY rats after 4 days of fasting and during unrestricted feeding (Fig. 1). Although fractional and calculated turnover rates were significantly slowed by fasting in both strains, turnover rates did not differ in the two fed groups or in the two food-deprived groups. Fasting thus suppressed cardiac SNS activity to an equivalent extent in SH rats (-61 percent) and WKY rats (-65 percent), implying that mechanisms in addition to diminished SNS activity contributed to the greater hypotensive response of SH rats to fasting.