The Condor 92:582–586

DIVING BEHAVIOR OF ADÉLIE PENGUINS DETERMINED BY TIME-DEPTH RECORDER[1]

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Abstract. The diving behavior of Adélie Penguins, *Pygoscelis adeliae*, was investigated near Syowa Station during December 1986, with time-depth recorders attached to nesting birds caring for 2- to 3-week-old chicks. Three of four recorders were recovered 150–334 hr after attachment. Most (98%) of the 587 dives recorded were less than 20 m in depth and 40% occurred between 16:00 and 20:00. Mean depths ranged from 6.1–10.9 m and maximum depth was 16.9–26.8 m. Mean and maximum dive durations were 1.4–1.9 min and 2.7–4.0 min. Ninety-seven percent of dives occurred in 44 diving bouts that averaged 25.3 min and 12.9 dives per bout. Descent and ascent rates during dives were similar in 88% of dives, meaning that the penguins dived at low angles, averaging 5°.

Key words: Adélie Penguin; time-depth recorder; Antarctica; diving bout; diving profile; descent rate; ascent rate; diving angle.

INTRODUCTION

Several recent studies have focused on the foraging ecology of penguins. In order to advance our understanding of underwater behavior, a variety of depth recorders has been developed, including the autoradiographic depth gauge (Wilson and Bain 1984) and the multiple-maximum-depth recorder (MDR) (Kooyman et al. 1983). These instruments facilitate direct studies on the diving behavior of penguins, yielding the frequency and depth of dives during their foraging trips. Information from these instruments (Kooyman et al. 1983, Wilson 1985, Lishman and Croxall 1983, Croxall et al. 1988), combined with information obtained from diet analysis, have improved our knowledge of foraging penguin behavior. Still lacking is critical information on diving profiles, diving speed during descent and ascent, dive duration, and diving pattern as a function of time of day.

For a more detailed record of the penguin diving pattern, we developed small time-depth recorders and attached them to Adélie Penguins, *Pygoscelis adeliae*, at Mame Island 5 km west of Syowa Station, Antarctica (69°00′S, 39°35′E) in December 1986. This is a first report on the diving behavior of Adélie Penguins with these instruments.

MATERIALS AND METHODS

TIME-DEPTH RECORDER (TDR)

The TDR is 25 mm in diameter by 85 mm long and weighs 70 g in air. It is composed of three main parts: (1) recording paper and stylus, (2) bellows-type pressure transducer, and (3) quartz paper drive motor and gear shifts. Thin carbon-coated paper, 18 μ thick, combined with a slow initial winding rate of 0.04 mm/min, made possible by reducing the speed of the quartz motor, allowed for a record duration of 25 days. A diamond stylus, connected to the pressure sensor, etched a thin high-resolution line measuring less than 10 μ on the paper. The power source was a 3-V, bottom-type lithium battery (CR2023). The bellows-type pressure sensor is highly accurate even after repeated increases in pressure and shows negligible mechanical hysteresis. The depth range varies with the type of pressure transducer used; a 150-m range bellows-type pressure sensor was used for this study. The combination of parts used made a compact package that was usable on small diving birds.

[1] Received 4 September 1989. Final acceptance 26 April 1990.

TABLE 1. Summary statistics from diving records of three Adélie Penguins.

Penguin number	Record duration time (hr)	No. of dives	Dive duration time $\bar{x} \pm$ SD (min)	Dive duration time Maximum (min)	Diving depth $\bar{x} \pm$ SD (m)	Diving depth Maximum (m)
8512 (19 Dec.–25 Dec.)	150	68	1.9 ± 0.49	3.6	8.2 ± 3.24	16.9
8514 (19 Dec.–2 Jan.)	334	378	1.7 ± 0.63	4.0	10.9 ± 4.80	26.8
8516 (21 Dec.–2 Jan.)	290	141	1.4 ± 0.37	2.7	6.1 ± 3.61	19.1
Total	774	587				
$\bar{x} \pm$ SD			1.7 ± 0.58		9.4 ± 4.82	

FIELD STUDY

The mode of attachment of the TDR was tested with Humboldt Penguins, *Spheniscus humboldti,* at Kamogawa Sea World (Kamogawa, Chiba, Japan). The TDR was attached with medical rubber tubing, 5 mm in diameter, that was wound crossways around the body. During 1 month of testing, no significant or visible effect of the TDR or the harness was noted. The subject behaved like other uninstrumented birds throughout the test period. However, we assume that the TDR and the harness might have affected the penguins' swimming ability that was not measured during the test period at the aquarium. Heath and Randall (1989) reported that the same type of harness (Wilson and Bain 1984) caused flippers to wear and affected mobility and swimming ability. Thus interference problems, particularly due to the harness, still remained.

Deployment of the experimental TDRs was conducted at the northern end of Mame Island, where 15–40 pairs of Adélie Penguins breed annually (Hoshiai et al. 1981, Kanda et al. 1986). On 19–21 December 1986, the TDRs were attached to four Adélie Penguins out of 21 pairs that were brooding young chicks. Three of the TDRs were recovered 7–15 days later. It was not possible to recover the fourth due to the bird's absence on our second recovery trip. No field observation was conducted during the period between attachment and recovery due to dangerous ice conditions. After recovery, the paper bearing the data was enlarged using a reader printer (Minolta RP507); the data were digitized, and analyzed by computer. Most dives occurred in clusters. To define these diving bouts, we used a log-survivor curve of surface intervals (Gentry and Kooyman 1986). A series of four or more dives not separated by a surface period exceeding 5 min was regarded as a diving bout.

RESULTS

DIVE DURATION AND DEPTH

We obtained complete records of both dive duration and dive depth from all three birds. These birds dived a total of 587 times during 774 hr of recording (Table 1). Record duration (i.e., period between deployment and recovery) was 150–334 hr. In the present study, unfortunately, we could not obtain any data on incubation shifts and length of trips to sea. According to Matsuda (1964), chick-brooding parents go to sea alternately at 1–2 day intervals. The present diving records may suggest such intervals in this area.

Most dives lasted between 1.0 and 2.0 min (65%); dives exceeding 3.0 min were very rare (Fig. 1). On the other hand, diving depth was more dispersed with an uncertain peak (Fig. 1). Dives exceeding 20 m were very rare (2%). Comparing the mean dive duration and depth (Table 1), the dive duration was more stable than dive depth individually or interindividually. The bird 8512 dived 1.12 and 1.36 times longer than others while the bird 8514 dived 1.33 and 1.79 times deeper than others.

DIVING BOUT AND PROFILE

The majority of dives (96.6%) occurred in 44 bouts (Table 2; Fig. 2a, b). Bouts averaged 24.4, 25.5, and 26.0 min and contained a mean of 11.4, 13.2, and 12.7 dives, for the three birds, respectively. The interval between dives in a bout averaged 2.1 min and varied little from one penguin to the next. The remainder of the dives occurred as single events widely separated in time. Dive depths within a bout of two birds were deeper

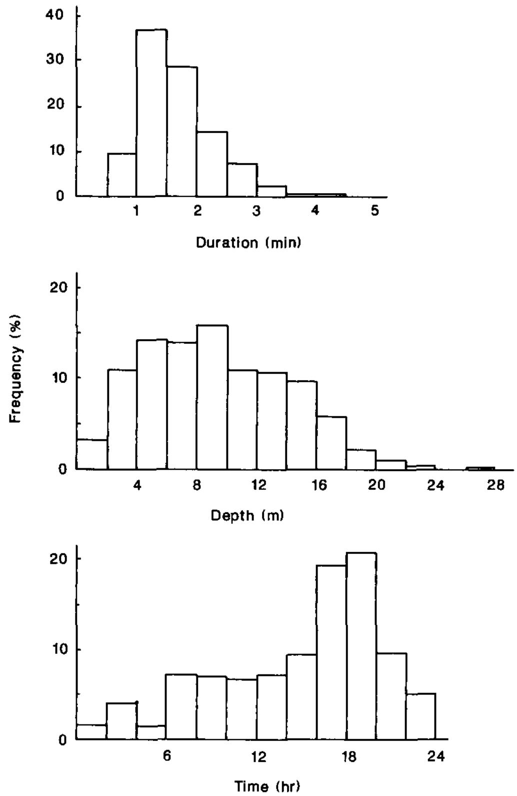

FIGURE 1. Frequency distribution of dive duration (top), dive depth (middle), and dive time (bottom) for three Adélie Penguins (587 dives).

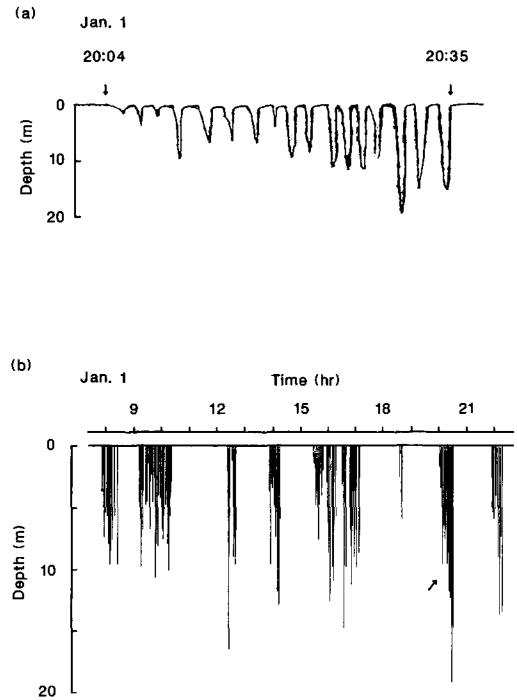

FIGURE 2. (a) Example of diving bout. Excerpt from diving record of Adélie Penguin No.8516. (b) Example of 11 diving bouts of Adélie Penguin No.8516. One line shows one dive. The diving bout which is indicated by an arrow corresponds to the diving bout of (a).

on average than independent dives by about 1.7 m and 4.9 m, respectively ($P < 0.05$, one-tailed Mann-Whitney U-test). One bird had no dives out of bouts.

In the present study, we examined the profiles of 587 dives and found that 88% showed a spiky profile (i.e., lacking clear time spent at bottom) with very similar descent and ascent rates.

DAILY DIVING PATTERN

Diving was observed at all hours of the day with peaks of diving activity between about 16:00 and 20:00; there were few dives (7%) between 00:00 and 06:00 (Fig. 1). There was a tendency for 40% of dives to be circumscribed by the limits 15:00–20:00 at 4–15 m in depth and 60% by 13:00–21:00 at 1–16 m in depth (Fig. 3).

DISCUSSION

EFFECT OF TDR ATTACHMENT

According to Wilson et al. (1986), traveling velocity of penguins decreases with the increasing cross-sectional area of the instrument carried. Using Wilson's formula (1986), Croxall et al. (1988) calculated 9% and 5–6% speed reduction in Macaroni Penguins, *Eudyptes chrysolophus,* and Gentoo Penguins, *Pygoscelis papua,* respectively, for the depth histogram recorders (DHR). The instruments used in the present study are 2.0 mm larger in diameter (and 25 g lighter than the DHR). We have no direct data on the cross-sectional area of an Adélie Penguin, but there is little difference in body size between Macaroni and Adélie Penguins. Using 14,000 mm^2, the estimate of the Macaroni Penguin's cross-sectional area (Croxall et al. 1988), in Wilson's formula, a 10.4% speed reduction might have occurred. We do not know how this might affect the foraging habits of our penguins.

DIVING MODE

The diving depth information for Adélie Penguins is scarce. Direct measurement of depth was done by Whitehead (1989) using capillary depth gauges which record the deepest depth an animal attains during a foraging trip. He reported 79 to

TABLE 2. Mean duration and number of dives in diving bouts of three Adélie Penguins.

Penguin number	Number of diving bouts	Bout duration time (min)		Dives per bout	
		Mean	Range	Mean	Range
8512	5	22.4	12.2–38.0	11.4	8–19
8514	27	25.5	8.1–76.3	13.2	4–32
8516	11	26.0	7.9–72.0	12.7	5–33
Mean		25.3		12.9	
SD		15.4		7.6	

175 m, 70 to 157 m, and 56 to 128 m as the ranges of maximum depth for breeding Adélie Penguins at three stages of chick growth. The depths, recorded in the present study are much shallower than those recorded by Whitehead (1989). They are also shallower than those attained by Chinstrap Penguins, *P. antarctica,* which are similar in size to Adélie Penguins. Ten percent of 1,109 Chinstrap Penguin dives were deeper than 45 m and 60% were shallower than 10 m (Lishman and Croxall 1983). Against dive depths, our data on maximum and mean dive duration were compatible to the enforced dive duration of 6.0 min for Adélie Penguins and to the dive duration of 1.5 ± 0.1 min for free-diving similar-sized Chinstrap Penguins recorded by Kooyman (1975) and Trivelpiece et al. (1986), respectively. We cannot give any clear explanation for the present shallow dives while the dive duration was maintained as long as other reports. We already pointed out the possibility of swim speed reduction due to the TDR. When speed reduction is eminent, this may cause the shallow dives with sustained effort in dive duration. However, the fact that Blue-eyed Shags, *Phalacrocorax atriceps,* which are about half the size of Adélie Penguins, and had the same TDRs attached on their backs dived deep, often exceeding 100 m in depth (Naito, unpubl.), may contradict the above explanation. Harness interference may cause the shallow dives. The same type of harness adopted by Wilson and Bain (1984) caused flipper wear and affected mobility and swimming ability (Heath and Randall 1989). We cannot deny the possibility that speed reduction is affected by this kind of interference. Despite this, we still cannot explain why dive duration was not affected as much as dive depth by such interference. Trivelpiece et al. (1986) reported 0- to 10-m shallow dives in swimming or researching dives of Chinstrap Penguins. Many of the present shallow dives may not be feeding dives, but are for swimming or searching. On the other hand, the birds apparently conducted successful feeding dives during the experimental period. All six chicks survived throughout the period. This means that the birds captured the prey in rather shallow waters. As indicated by Croxall et al. (1988), Fraser et al. (1989), and Whitehead (1989), diving behavior of penguins should be discussed in relation to food availability including type, density, and distribution of the prey in the foraging area, the extent of the bird's food requirement, and physiological diving capacity. In the present study, we did not examine stomach samples nor levels of food requirement. Therefore, we are unable to explain the shallow diving from the viewpoint of foraging at present.

DIVING BOUT AND PROFILE

This is the first time that TDRs have been used to record the diving behavior of free-living Adélie Penguins. Because this instrument provides a continuous record of diving against time use, we discovered that nearly all diving was concentrated into bouts lasting less than 30 min followed by swimming or resting periods at the surface or on the ice. We did not observe the incubation shifts at the nests. However, from the dive records, we predicted the bout frequency on a foraging trip. The birds 8512, 8514, and 8516 had a mean number of 2.5, 5.5, and 11 bouts on a foraging trip. We do not know whether these dives were sufficient to capture the required amount of prey for the chicks and themselves. We still need information on their feeding.

The way in which the penguin diving patterns that we observed reflected the distribution of the penguins' prey is unclear. The mean duration of the Adélie Penguin's dives was 1.7 min and the mean depth was 9.3 m. Taking the figure of 7.2 km/hr as swimming velocity (Kooyman 1975), the distance covered during an average dive is about 204 m. Because 88% of dives showed almost an equal descent and ascent rate (Fig. 2a), this suggests that these Adélie Penguins' diving angle was, at 5° from the horizontal, very shallow. This would be consistent with feeding on

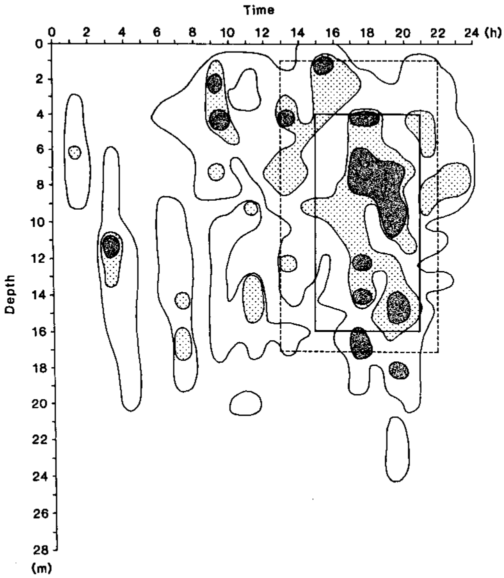

FIGURE 3. Frequency distribution of diving time-depth relationships for three Adélie Penguins (shaded area ≥5 dives, stippled area = 3–4 dives, plain area = 1–2 dives). The areas framed in solid and dotted line show 40% and 60% of total dives, respectively.

shallow prey, but also with the long swimming dives noted by Trivelpiece et al. (1986).

DIVING PATTERN

The diving patterns of Gentoo and Macaroni penguins have been studied in relation to the vertical movement of Antarctic krill (Croxall et al. 1988). Macaroni Penguins make shallow dives of less than 20 m at night, but some deeper ones at night and in the daytime. In our study, the deepest dives were in the late afternoon and evening. This species difference in foraging time is no doubt due to differences in environment. During the study at Mame Island, the sun never set whereas it did set at South Georgia, located at 54°S. In the Ross Sea, south of Mame Island (hence the sun does not set during summer), Ainley et al. (1984) found as we did that a peak in Adélie Penguin foraging occurred at 18:00–20:00, as well as at 03:00–05:00.

ACKNOWLEDGMENTS

We are grateful to the members of the wintering party of the 27th Japanese Antarctic Research Expedition for their help in the field, and Mr. Sakurai, National Institute of Polar Research, for his valuable assistance in the computer data processing.

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