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DIVING PATTERN AND PERFORMANCE IN NONBREEDING GENTOO PENGUINS (*PYGOSCELIS PAPUA*) DURING WINTER

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ABSTRACT.—We studied diving patterns and performance (dive depth, duration, frequency and organization during the foraging trip) in relation to diet in nonbreeding Gentoo Penguins (*Pygoscelis papua*) over 59 days (involving 5,469 dives) in winter. We estimated foraging ranges and prey capture rates, and compared foraging behavior with that of breeding (chick-rearing) birds. Foraging was highly diurnal with 98% of foraging trips completed during the same day. Foraging-trip frequency was 0.8/day, trip duration was 6-8 h, and birds spent 51-62% of the foraging trip diving. Dive depth and duration were bimodal. Shallow dives (<21 m; 42% of total number and 16% of total dive time) averaged 5-7 m and 0.5-1.3 min. Deep dives (>30 m; 55% of total number and 81% of dive time) averaged 74-105 m and 2.7-3.5 min, respectively. Deep-dive duration exceeded the subsequent surface interval, but shallow dives were followed by surface intervals two to three times dive duration. Deep dives showed clear diel patterns, averaging 10-20 m at dawn and dusk and 70-90 m at midday. These results are consistent with the patchy vertical and horizontal distribution and diel movements of Antarctic krill, the main winter prey of Gentoo Penguins (including study birds). We suggest that shallow dives are mainly searching dives, and deep dives mainly for feeding. Foraging activity of nonbreeding Gentoo Penguins in winter is similar to that of chick-rearing birds. The only major differences are that foraging-trip frequency is 20% less and stomach-content mass on return ashore 30% less in winter. We conclude that foraging activity in Gentoo Penguins is changed by varying the frequency and duration of foraging trips, rather than by changing the pattern and rate of diving. *Received 6 December 1990, accepted 10 January 1992.*

SEABIRDS, and in particular penguins (Spheniscidae), are a major component of the predator-prey system in the Southern Ocean (Croxall 1984, Everson 1984, Croxall and Prince 1987). However, most of our knowledge of such birds derives from breeding-season studies and still very little is known about their ecology during the nonreproductive period (Croxall et al. 1984). Until recently, information on the activity of seabirds at sea (during both breeding and nonbreeding periods) has been very difficult to obtain (Ellis 1984). In the last few years, a range of small devices have been developed to record directly foraging behavior of free-ranging birds at sea. However, so far these have been deployed exclusively on breeding (mainly chick-rearing) birds and, except for the study of Naito et al. (1990), have only provided data on one or two aspects of diving behavior (e.g. maximum dive depth or number of dives to defined depths; Kooyman et al. 1982, Adams and Brown 1983, Lishman and Croxall 1983, Wilson and Bain 1984, Croxall et al. 1988a, Gales et al. 1990).

In many avian species, energy expenditure peaks during the reproductive period with the additional energy requirements associated with production of young. Although energy expenditure may be relatively low in nonbreeding birds during the winter, costs of energy acquisition (foraging rates) may be high (Walsberg 1981). In winter, food availability may be lower and, for diurnally foraging species, less time is available to forage due to decreased daylengths. Data on seasonal changes in foraging ecology and foraging effort are only available for a few species (e.g. Walsberg 1978, Mugaas and King 1981).

We present information on diving patterns and performance (dive depth, duration, frequency and organization during foraging trips)

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of nonbreeding Gentoo Penguins during winter, together with data on winter diet obtained from both instrumented and noninstrumented birds. We use these data to estimate foraging ranges and prey capture rates for nonbreeding birds. Finally, using similar data collected in the breeding season by Williams et al. (1992), we compare seasonal variation in foraging behavior in breeding and nonbreeding Gentoo Penguins in order to assess the effect of chick-rearing on foraging effort.

METHODS

Field methods and dive recorders.—Diving behavior was studied with time-depth recorders (TDRs) at the Johnson Cove colony, Bird Island, South Georgia (54°00'S 38°02'W) during the 1989 austral winter. Five TDRs were deployed in July 1989, of which three were recovered and had recorded data. Two birds (one male, bird 8A; one female, bird 9A) received microprocessor-controlled Wildlife Computers Mk III+ recorders (Wildlife Computers, Woodinville, Washington). These had a 128-Kbyte memory and recorded discontinuously with a sampling interval of 15 s and a minimum depth threshold of 2 m. They measured 100 mm (length) by 35 mm (width) by 16 mm (height), and weighed 90 g in air (1.5% of Gentoo Penguin mass). Data from these recorders, which were deployed between 2-21 July 1989, were downloaded directly to computer. The third bird (a female, bird 41) received a mechanical, continuously-sampling device developed by the National Institute of Polar Research (NIPR) in Japan. This was deployed on 3 July and recovered on 25 September; data were recorded until 24 July. Full details of the NIPR recorders and the analytical procedures used are given in Naito et al. (1989, 1990). The NIPR recorders measured 25 mm (diameter) by 85 mm (length), and weighed 73 g in air (1.2% of penguin mass). Devices were attached to the birds' back feathers with quick-set epoxy resin (RS Components, Corby, Northamptonshire, United Kingdom). They recorded: date; time; the number, depth and duration of each dive; and the surface interval between successive dives. In addition, the NIPR recorder produced a continuous profile for each dive and, therefore, it was possible to estimate the amount of time spent at maximum depth for each dive. All three birds had been banded as breeding adults in October 1986 and, thus, were known to be at least four years old at the time recorders were attached.

Data analysis and interpretation.—Due to differences in the recording system and sampling interval between the two recorder types, some differences occurred in the dive records they produced. Specifically, the NIPR devices recorded a smaller number of shallow dives (<21 m) with proportionately greater durations for the same dive depth due to concatenation of some very shallow dives with short surface intervals (Williams et al. 1992). However, there were no analagous differences in the recorded total time spent in shallow dives or in the number of, or time spent in, deep dives (>30 m). We present data for the three individual birds separately.

The initial unit of analysis was the daily foraging period, defined as the time between the first and last dive in a day. The longest surface intervals (with no recorded diving) within this foraging period were 60, 100 and 120 min for the three individual birds. We assumed that birds remained at sea during the whole foraging period (see Williams et al. 1992). This was supported by radio-telemetry data on winter activity patterns obtained at the same colony in 1988 (Williams 1991). In our study, the birds made only one foraging trip per day, and this was equivalent to the daily foraging period.

Of 47 foraging trips, 46 (98%) were completed in the same day, but one trip by one bird (8A) lasted overnight. As overnight trips are very rare (none recorded by Williams et al. 1992) and this single trip had a disproportionately large effect on the coefficient of variation for all variables (see also Williams and Rothery 1990), we analyzed it separately. Only foraging trips with a minimum of 20 dives were included in the main analysis.

To analyze the organization of diving within foraging trips, we plotted survivorship curves of surface intervals (Gentry and Kooyman 1986) to identify bout-ending criteria, which delimited bouts of diving activity. However, this method failed to indicate any inflexion points. Consequently, we could not identify dive bouts within foraging trips.

Statistical tests were performed in Minitab (Ryan et al. 1985) or SAS (SAS Institute 1985). Times are given as hours, local time (which is G.M.T. minus 2 h). Daylength (including civil twilight) during the deployment period was 8.9-9.6 h. On 3 July, sunrise was at 0732 and sunset at 1628. On 21 July, sunrise was at 0712 and sunset at 1648.

Estimation of travel time and foraging range.—We estimated time spent travelling in two ways. First, we assumed that birds travelled continuously while at the surface. Second, we added to this the time spent in shallow dives (calculated as total time minus time spent in deep dives), assuming that all shallow dives involve only travel (see later). We estimated the foraging range by calculating the time elapsed between the first recorded dive (>2 m) and the first dive deeper than 20 m (i.e. assuming that shallow dives are nonfeeding dives), and assuming that birds travelled continuously and in a straight line (Heath and Randall 1989). We calculated the time between the last dive deeper than 20 m and the last dive to give a foraging range based on the return journey. From direct observations on four birds, the time between entering and leaving the water, and the first or last recorded dive averaged 20 min (range 3-45 min). We added this time to all estimates of travel time. For all estimates, swimming speed was taken as 2.2 m/s (Wilson et al. 1989b).

Food sampling and analysis of diet.—Stomachs of birds 8A and 9A were sampled on 21 July as the birds returned to the colony after the last recorded foraging trip. In addition, food samples were obtained from 10 noninstrumented birds on 11-12 July and 6 birds on 22 July. All food samples were obtained by complete flushing of the stomach (Wilson 1984, Jablonski 1985, Gales 1987). Analysis of food samples was as described by Williams (1991), except that weights of individual Antarctic krill (*Euphausia superba*) were calculated from age- and sex-specific equations given in Morris et al. (1988).

RESULTS

Effect of instrument.—Williams et al. (1992), based on data on activity patterns, foraging trip duration, breeding success and chick growth rates, concluded that these recorders did not have a marked effect on foraging behavior of chick-rearing Gentoo Penguins. Wilson et al. (1986), Croxall et al. (1988a) and Gales et al. (1990) also found no significant difference in foraging-trip duration or the mass of prey brought ashore between instrumented penguins and control birds with devices the same size (or larger) than those used in our study, although instrumented birds may have a greater energy expenditure. The cross-sectional area of the WI and NIPR devices was equivalent to 2.7% and 2.3%, respectively, of the cross-sectional area of a Gentoo Penguin. This could represent a decrease in swimming speed of 6% to 7% (Wilson et al. 1986). However, devices used by Wilson et al. (1986, 1989a) were not streamlined, and the hydrodynamically-shaped proximal end of the TDRs we used would substantially reduce any increased drag (Kooyman 1989). In our study, there was no difference in the frequency of foraging trips compared to values obtained for Gentoo Penguins with radio transmitters during winter 1988 at South Georgia (Williams and Rothery 1990), but two of the three birds made, on average, significantly longer foraging trips (t-test, $P < 0.01$). The total weight and gross composition of stomach samples from the two Gentoo Penguins with recorders were within the range of values obtained from noninstrumented birds sampled at the same time (Table 1). However, there were significant differences in the proportions of different krill types taken and in the size of adult male, but not female or juvenile, krill taken. Birds with recorders took fewer, and smaller, male krill than noninstrumented birds (Table 1). It is not possible to determine whether these differences indicate an effect of the recorders on diving performance, or whether the differences simply reflect annual or individual variation, or both, in foraging behavior.

TABLE 1. Total weight (g), composition (%) and proportion (%), as well as length (mm) and weight (g) for different sex and age classes, of krill in food samples obtained from Gentoo Penguins with WI-type time-depth recorders (TDRs) and noninstrumented birds. Data taken 21 and 22 July 1989. Values are ranges (mean in parentheses) or means ± SD.

	TDR bird		Non-TDR birds ($n = 6$)
	8A	9A	
Total weight	179.3	466.2	179.1-779.3 (540)
Percent krill	100.0	100.0	63.3-100.0 (95)
Percent fish	0.0	0.0	0.0-36.7 (5)
Proportion (no.) of krill[a]			
Adult male	48.0 (84)		63.5 (376)
Adult female	45.1 (79)		28.0 (166)
Juvenile	6.9 (12)		8.5 (50)
Krill length			
Adult male[b]	51.1 ± 3.0		53.0 ± 3.2
Adult female	47.9 ± 3.1		48.3 ± 3.3
Juvenile	45.1 ± 3.8		45.4 ± 7.1
Krill weight			
Adult male[b]	1.11 ± 0.19		1.24 ± 0.22
Adult female	0.77 ± 0.13		0.79 ± 0.14
Juvenile	0.77 ± 0.20		0.84 ± 0.37

[a] Significant difference between TDR and non-TDR birds, $X^2 = 18.21$, $P < 0.001$.

[b] Significant difference between TDR and non-TDR birds, t-test, $P < 0.001$.

Frequency, timing and duration of foraging trips.—We obtained data on the three instrumented birds for 59 days and 47 foraging trips (average 0.80 trips/day). The three birds remained in the colony (or made trips of fewer than 20 dives) on 2 of 21 (10%; bird 41), 2 of 19 (11%; bird 8A) and 7 of 19 (37%; bird 9A) days; all birds made only one foraging trip per day. Foraging behavior was highly diurnal (Fig. 1), and 46 of 47 foraging trips were completed within the same day (maximum duration 9.6 h). One lasted overnight (bird 8A, duration 32.6 h). No foraging trips were started before sunrise (0712), and 36 of 47 (77%) trips were completed before sunset

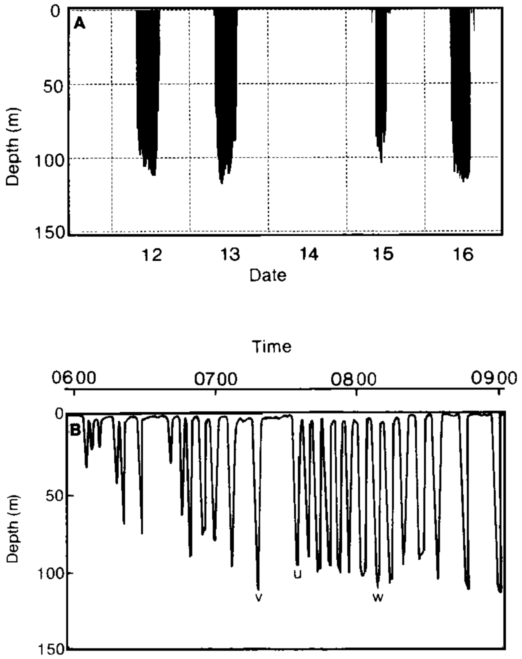

Fig. 1. (A) Part of diving record for an individual Gentoo Penguin (NIPR TDR 41) and (B) an enlarged section showing three types of dive profiles (*V*-, *W*- and *U*-shaped) obtained from NIPR recorder. Dates are calendar days in July.

(1648). Bird 9A arrived at the colony after sunset on one trip (28 min later) and bird 41 on six trips (18 min later). Three at-sea periods (1, 36, and 44 min) of fewer than 20 dives were recorded (all by bird 9A).

There was significant variation (ANOVA, $P < 0.05$) between individuals in foraging trip duration, total number of dives per trip, dive frequency (dives/h), and proportion of the trip spent diving (Table 2). In addition, birds 8A and 9A had significantly different mean trip duration ($t = 2.21$, $P < 0.05$), dive frequency ($t = 4.21$, $P < 0.001$), and proportion of the trip spent diving ($t = 2.45$, $P < 0.05$). These differences were due to individual variation rather than to differences in the type of recorder carried. Mean foraging-trip duration for the different individuals ranged from 6.0–8.4 h; birds spent on average 25–35% of each day, and 65–91% of available daylength, at sea. The proportion of the foraging trip spent diving (i.e. potential feeding time) averaged 51–62% and represented 3.4–4.6 h per day.

For diurnal foraging trips, mean total dive frequency was 12–25 dives/h (Table 2). For the overnight trip, during darkness, bird 8A made 70 dives in 14.4 h (5 dives/h); between 2200 and 0300, it made only 9 dives (2 dives/h).

Dive depth, duration and surface intervals.—In general, we distinguished two main types of dives (Figs. 2 and 3; Table 3). Shallow dives (averages for individual birds range from 5–7 m) of short duration (averages 0.5–1.3 min) and deep dives (averages 74–105 m) of long duration (averages 2.7–3.0 min), with fewer than 3% of dives intermediate between these categories. The comparatively reduced frequency of short and shallow dives by bird 41 reflects concatenation of such dives by the NIPR recorder. We

TABLE 2. Data on foraging trips (frequency, timing and duration), dives (number and frequency), and proportion of foraging trip spent diving in Gentoo Penguins. Values are means ± SD, with ranges in parentheses. Values for TDR 8A exclude the single overnight trip (see text).

	TDR number		
Characteristic[a]	41	8A	9A
Instrument type	NIPR	WI	WI
No. days	21	19	19
No. foraging trips	19	15	12
Foraging trip frequency	0.905	0.789	0.632
Departure time	08.06 ± 54	08.13 ± 15	08.21 ± 25
Arrival time*	14.40 ± 38	16.36 ± 55	14.21 ± 151
Foraging trip duration (h)**	6.6 ± 0.9	8.4 ± 0.9	6.0 ± 2.6
	(4.2–8.0)	(6.6–9.6)	(1.2–9.0)
No. dives per trip**	78 ± 26	140 ± 17	140 ± 58
	(47–143)	(120–175)	(39–228)
Dive frequency (dives/h)**	12 ± 3	17 ± 3	25 ± 6
	(7–18)	(13–23)	(19–40)
Percent of trip spent diving*	51 ± 13	55 ± 6	62 ± 10
	(31–69)	(47–68)	(44–77)

[a] Significant difference among individuals (ANOVA). * $P < 0.05$. ** $P < 0.01$.

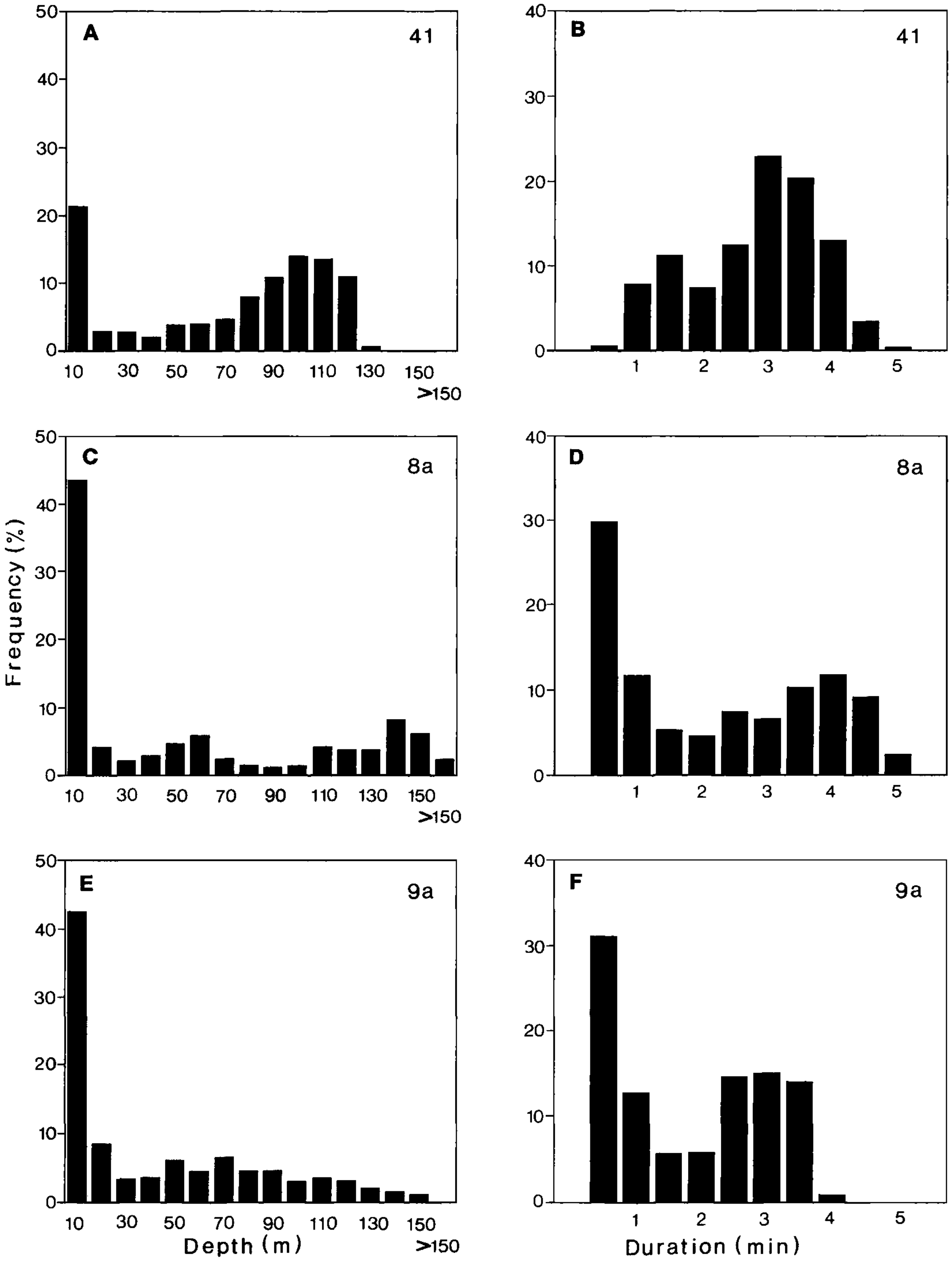

Fig. 2. Frequency distribution of dive depth and dive duration in Gentoo Penguins in winter.

classified dives as deep (>30 m), intermediate (21-39 m), and shallow (<21 m), analyzing each category separately (Williams et al. 1992). The proportions of deep, intermediate and shallow dives (based on number of dives) were: 73%, 3% and 24% for bird 41 (*n* = 1,489); 50%, 2% and 48% for bird 8A (*n* = 2,304); and 46%, 4% and 50% for bird 9A (*n* = 1,676). The mean depth

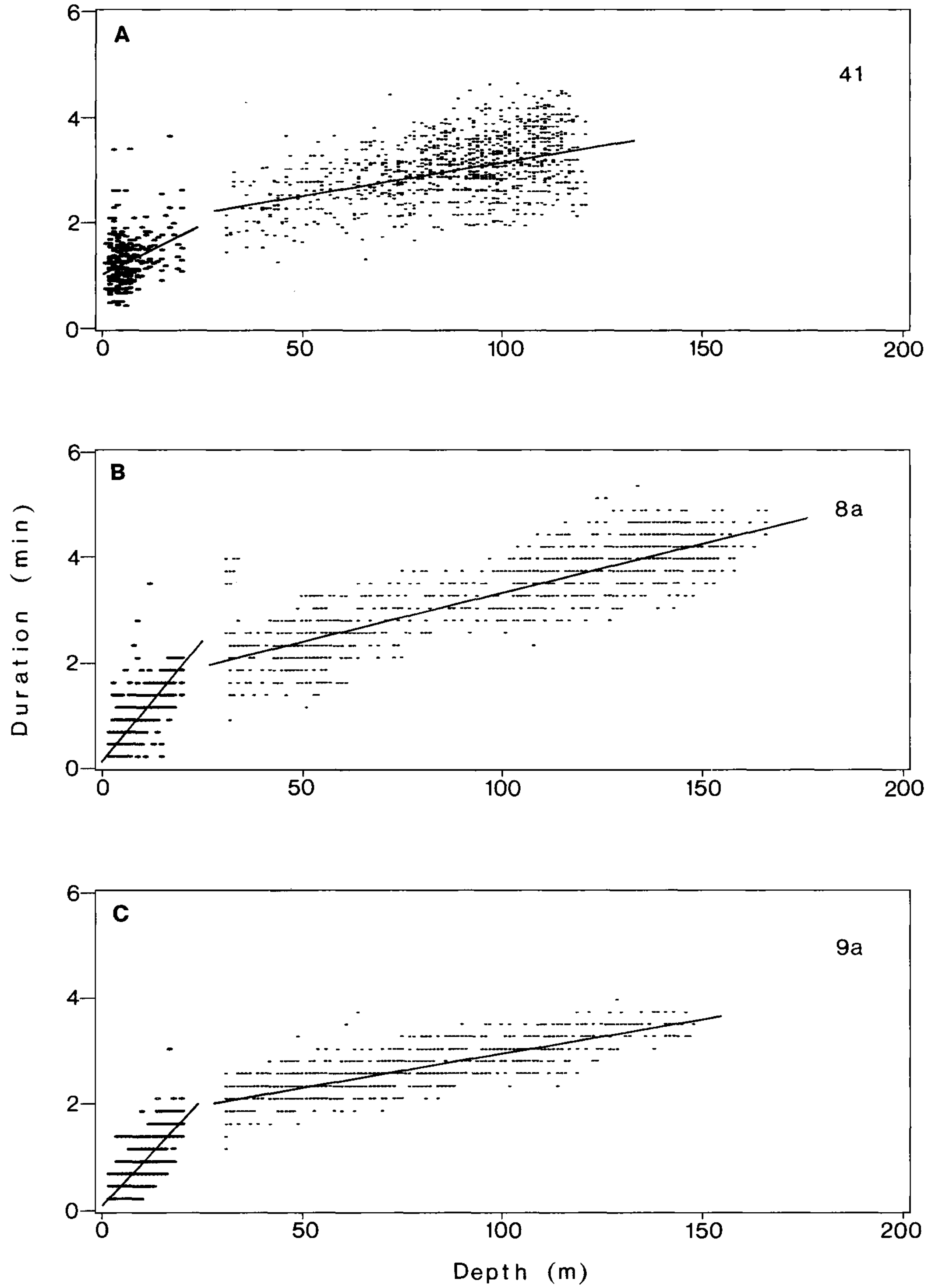

Fig. 3. Relationship between dive duration and dive depth for deep (to right) and shallow (to left) dives in Gentoo Penguins. Least-squares regression equations are: (A) NIPR TDR 41, deep, $Y = 1.91 + 0.01X$; shallow, $Y = 1.00 + 0.04X$. (B) WI TDR 8A, deep, $Y = 1.50 + 0.02X$; shallow, $Y = 0.12 + 0.09X$. (C) WI TDR 9A, deep, $Y = 1.69 + 0.01X$; shallow, $Y = 0.07 + 0.08X$.

TABLE 3. Frequency of deep (>30 m; $n = 3{,}010$), intermediate (21–30 m; $n = 158$), and shallow (<21 m; $n = 2{,}301$) dives by Gentoo Penguins; proportion (%) of foraging trip spent diving in each category and depth (m); duration (min) and surface interval (min) between dives for each category. Values are means ± SD. Sample sizes of foraging trips and instrument types as given in Table 2.

		Dive category[a]		
Variable	TDR bird	Deep	Intermediate	Shallow
Dives/h	41	8.7 ± 2.0	0.4 ± 0.7*	2.8 ± 2.3**
	8A	8.6 ± 3.2	0.3 ± 0.3	7.9 ± 3.2
	9A	10.0 ± 4.4	1.1 ± 0.9	13.7 ± 9.2
Percent trip	41	43.8 ± 10.2	1.3 ± 2.5*	5.9 ± 4.6**
	8A	46.5 ± 7.4	1.0 ± 0.8	7.2 ± 2.9
	9A	44.2 ± 17.9	3.2 ± 2.3	14.5 ± 8.9
Depth	41	89.1 ± 15.7**	24.8 ± 2.2	6.4 ± 2.1**
	8A	104.7 ± 31.5	25.4 ± 2.7	4.8 ± 0.6
	9A	73.5 ± 23.7	25.2 ± 1.4	7.1 ± 1.4
Duration	41	3.0 ± 0.4**	1.9 ± 0.4	1.3 ± 0.3**
	8A	3.5 ± 0.7	1.9 ± 0.4	0.5 ± 0.1
	9A	2.7 ± 0.3	1.9 ± 0.2	0.6 ± 0.1
Interval	41	2.4 ± 1.0**	4.8 ± 7.4	5.1 ± 6.8*
	8A	1.7 ± 0.5	1.8 ± 1.4	1.7 ± 0.5
	9A	1.0 ± 0.6	1.0 ± 0.9	1.1 ± 0.5

[a] Significant difference among the three individuals (ANOVA). * $P < 0.05$. ** $P < 0.01$.

of deep dives was 89 m, 74 m and 105 m in the three birds (Table 3), and this varied significantly (ANOVA, $P < 0.01$) among individuals. The deepest dive recorded was 166 m; 32% (bird 41), 14% (bird 8A) and 30% (bird 9A) of all dives exceeded 100 m. Mean depth of deep dives varied with time of day (Fig. 4). The average depth was 10–30 m at dawn and dusk and 75–85 m in the middle of the day (1200–1400).

Dive duration (Table 3) for deep and shallow dives was positively related to dive depth (least-squares regression, $P < 0.001$) for all birds (Fig. 3). Dive depth accounted for 22% (bird 41), 72% (bird 8A) and 62% (bird 9A) of the variation in deep-dive duration, and 10%, 63% and 67% of the variation in shallow-dive duration.

The proportion of total foraging-trip time spent in deep dives was 44–46% and did not differ between individuals, but there was significant individual variation in the proportion of time spent in shallow dives: 6–15% (Table 3). Gentoo Penguins spent 85–86% (birds 41 and 8A) and 71% (bird 9A) of total diving time in deep dives, and 12–13% (birds 41 and 8A) and 23% (bird 9A) in shallow dives. They made 9 to 10 deep dives per hour and 3 to 14 shallow dives per hour (Table 3).

Mean surface intervals between dives varied from 1–5 min (Table 3). Average dive-to-pause ratios (i.e. dive duration/duration of subsequent surface intervals; from Table 3) were 1.2–2.7 for deep dives and 0.3–0.5 for shallow dives. Therefore, for deep dives the dive duration exceeded the subsequent surface interval, but shallow dives were followed by intervals two to three times dive duration.

Dive profile.—Continuous-dive profiles were available for 1,489 dives for bird 41. We identified three types of dive profile (Fig. 1): *V*-shaped (89% of all dives), *W*-shaped (4%), and *U*-shaped (7%). The *V*-shaped dives accounted for 97% of all shallow dives and 86% of all deep dives. For *U*-shaped dives, time at maximum depth was on average 22% of total dive duration (3.6 min).

Travel time and foraging range.—The estimated total distance travelled per foraging trip, based on total surface time (Table 4), averaged 27 km and was significantly different among individuals (ANOVA, $P < 0.01$). Adding the time spent in shallow dives (i.e. assuming this also represented travel time) increased the estimate of total distance travelled by 3–6 km ($\bar{x} = 5$ km or 19%). Estimated foraging range, based on time to the first 20-m dive, was 6.0 km (range 4.8–7.9 km). For the return journey, from the last 20-m dive, the same distance was 9.2 km (range 7.1–12.7 km).

Prey consumption and prey capture rates.—Stomach contents of TDR birds 8A and 9A yielded 100% Antarctic krill (Table 1). Samples from noninstrumented birds on the same days were

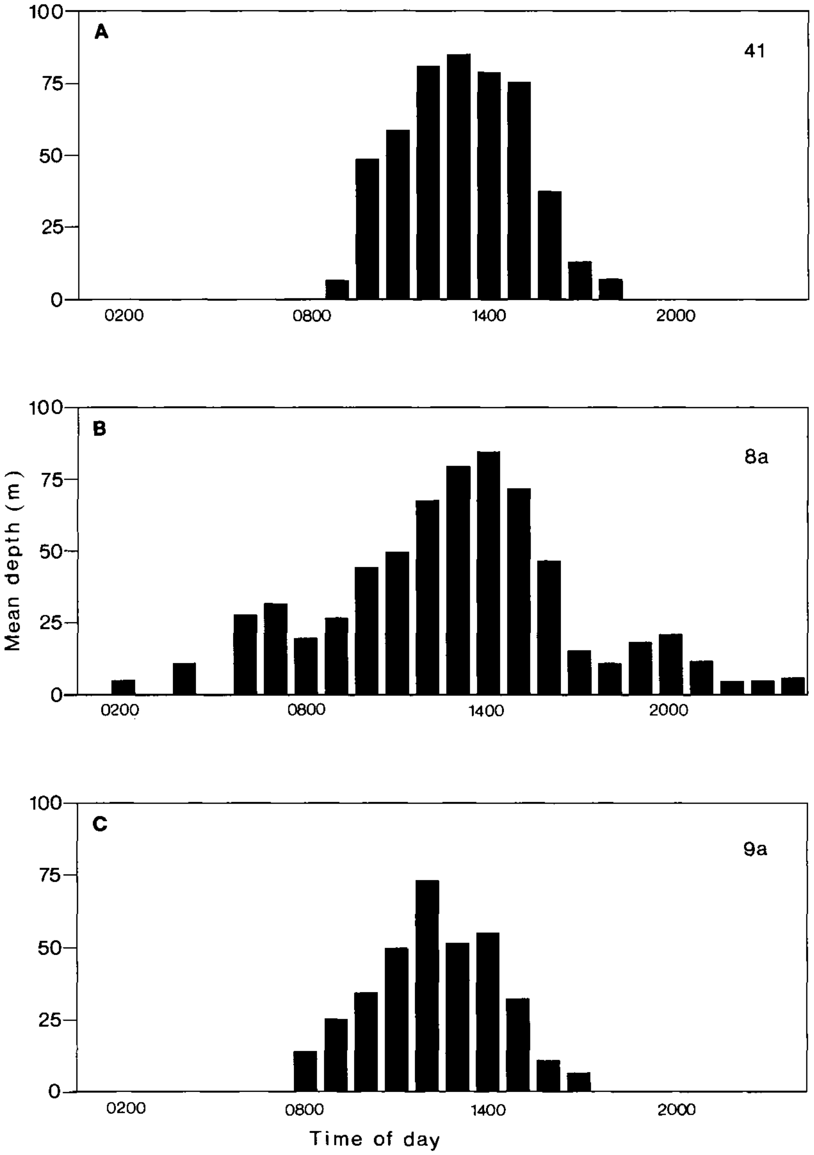

Fig. 4. Variation in mean depth of deep dives (>30 m) with time of day for Gentoo Penguins in winter.

comprised of 95% krill (Table 1). For the last foraging trip (21 July) of each of these TDR birds, we counted the krill consumed (313 and 766 individuals), estimated their total weight (284 g and 735 g) using length data (Table 5), and calculated potential prey-capture rates (Table 5). These ranged from 2–4 krill per dive to 1–3 krill per min if feeding occured only on deep dives. Bird 8A had a higher proportion of deep dives (81%) than bird 9A (56%). However, because bird 8A only consumed 41% by number and 39% by weight of the krill eaten by bird 9A, the former's prey-capture rates were substantially lower (Table 5).

Mean stomach-content weight of noninstrumented Gentoo Penguins on 11–12 July was significantly lower than that of birds sampled on 22 July (150 ± 49 g vs. 543 ± 204 g; $t = 4.41$, $P < 0.01$). In addition, on 11–12 July stomach samples comprised 26% crustaceans and 74% fish (by wet weight) compared to 95% crustaceans and 5% fish on 22 July. This suggests that the

TABLE 4. Estimated travel times (h) and distances (km) of Gentoo Penguins.

	41		8A		9A	
Method	Time	Distance	Time	Distance	Time	Distance
Nondive time[a]	3.6 ± 0.9	28.5	4.2 ± 0.8	33.3	2.6 ± 1.0	20.6
Nondeep dive time[a]	4.0 ± 0.8	31.7	4.9 ± 0.9	38.8	3.4 ± 1.3	26.9
Time to 20-m dive	0.6 ± 0.4	4.8	0.7 ± 0.4	5.5	1.0 ± 0.5	7.9
Time from 20-m dive	1.0 ± 0.6	7.9	1.6 ± 1.1	12.7	0.9 ± 0.7	7.1

[a] Significant difference among individuals (ANOVA). $P < 0.01$.

amount and type of food available during the period of TDR deployment may have changed. We investigated whether this was reflected in a change in the temporal pattern of four parameters of diving activity (trip duration, total time spent diving, percentage of diving time spent in deep dives, and mean depth of deep dives) over the deployment period. Although there was a significant trend with time in most of these variables (Spearman rank correlation), the pattern of change was not consistent among the different variables or among individuals (Table 6).

DISCUSSION

Winter foraging ecology in relation to diet.—At South Georgia, Gentoo Penguins feed predominantly on Antarctic krill, in both summer (Croxall et al. 1988a, b) and winter (Williams 1991, this study). Antarctic krill is a pelagic species that occurs mainly at depths of 80–120 m (but sometimes up to 20 m) during daylight hours, and forms dense swarms that are patchily distributed both vertically and horizontally (Everson 1982). The pattern of diving activity in nonbreeding Gentoo Penguins in winter is consistent with this distribution of their preferred prey and, consequently, is very similar to that of breeding birds (see below). Williams et al. (1992) suggested that shallow dives (<21 m) made by Gentoo Penguins are primarily searching dives used to locate krill swarms. If these are unsuccessful, the bird travels some distance horizontally before making the next searching dive. This explains the relatively long surface intervals between shallow dives, which also were characteristic of our study. Conversely, we assume that once a krill swarm is located the bird will maximize the time spent underwater and make repeated deep dives with relatively short surface intervals. Most deep dives would be mainly feeding dives, and the mean depth of these dives (74–105 m in this study) corresponds with the known vertical distribution of krill swarms. Furthermore, the large variation in depth of deep dives (coefficient of

TABLE 5. Estimated consumption of krill and prey capture rates for two individual foraging trips made by Gentoo Penguins (with WI-type recorders). Krill lengths and weights are means ± SD.

	TDR bird	
	8A	9A
No. krill ingested	313	766
Krill length (mm)	49.0 ± 3.7	49.4 ± 3.6
Krill weight (g)	0.91 ± 0.24	0.96 ± 0.23
Weight of krill ingested (g)	284	735
Foraging trip duration (h)	6.6	7.4
Time spent in deep dives (h)	4.2	4.1
Total no. dives	144	182
No. deep dives	116	102
No. krill/min deep dive time	1.3	3.1
No. krill per dive	2.2	4.2
No. krill per deep dive	2.7	7.5

TABLE 6. Temporal changes in four parameters of diving activity in Gentoo Penguins during study period. Spearman rank correlations coefficient and significance levels. Overnight foraging trip omitted for bird 8A.

		TDR bird		
Characteristic		9A	8A	41
Foraging-trip duration	r_s P	0.671 <0.01	−0.305 <0.01	−0.079 ns
Total time spent diving	r_s P	0.650 <0.01	0.253 <0.05	−0.549 <0.01
Percent diving time spent in deep dives	r_s P	0.643 <0.01	0.209 <0.05	0.342 <0.01
Mean depth of deep dives	r_s P	0.524 <0.01	−0.305 <0.01	0.465 <0.01

TABLE 7. Various characteristics of foraging activity and diving behavior in Gentoo Penguins at South Georgia during breeding[a] (chick-rearing) and in winter. Values are range of means of individual birds.

Characteristic	Breeding	Winter
No. birds (trips)	5 (74)	3 (47)
Foraging trips/day	0.80	0.97
Foraging-trip duration (h)	6.9–8.0	6.0–8.4
Total time spent diving (h)	2.5–5.4	3.4–4.6
No. total dives/h	18–26	12–25
No. deep dives/h	6.0–12.8	8.6–10.0
Mean depth of deep dives (m)	69–99	74–105
Estimated foraging range (km)	4–7	5–8
Stomach-content mass (g)[b]	775	540
Prey capture rate of krill (no. per deep dive)	13	8

[a] From Williams et al. (1992).

[b] Of birds feeding predominantly on krill.

variation 18–32%, Table 3) could reflect the highly variable vertical distribution of Antarctic krill. Finally, the diel pattern of mean dive depth (Fig. 4) mirrors the natural diel migration of krill (Kalinowski and Witek 1980, Everson 1982). The pattern of diving behavior we report for nonbreeding Gentoo Penguins is entirely consistent with the interpretation that deep dives are primarily feeding dives associated with krill swarms. Estimated foraging ranges were the same during summer (Williams et al. 1992) and winter (4–8 km). Gentoo Penguins continue to forage predominantly inshore in winter, even though they are not constrained by breeding activities to return regularly to the colony.

From the diet analysis we found evidence of a change in the type and abundance of prey available to Gentoo Penguins during the study period. Stomach samples obtained early in the deployment period had low weights (150 g) and consisted primarily of fish, whereas those collected at the end of the period were heavier (540 g) and consisted predominantly of krill. Williams (1991) also reported low weights and an increased proportion of fish in stomach samples of Gentoo Penguins during part of the 1987 winter at South Georgia. He suggested that this was due to local, decreased availability of krill. In situations of decreased food availability, Gentoo Penguins might increase the time spent trying to obtain food (i.e. time spent diving should increase). Assuming that food availability was lower early in the study period, there was only partial support for this hypothesis. In bird 41, time spent diving did decrease with time but the reverse was true for birds 8A and 9A, whose foraging trips were longest when krill was apparently most available (Table 6). This suggests an alternative hypothesis that, depending on a bird's body condition and time since last foraging trip, birds increase their foraging effort during periods of high food availability to capitalize on the abundant food supply.

These results have implications for suggestions that foraging-trip duration might be a good index of foraging effort, in relation to food supply, for use in monitoring studies of penguins and other seabirds (Croxall 1989, CCAMLR 1990, Williams and Rothery 1990). In our study, the relationship between time (days) and foraging-trip duration or time spent diving had the same slope in bird 9A (both positive) and bird 41 (both negative; Table 6). However, for bird 8A foraging-trip duration decreased over time, but total time spent diving increased. This suggests that foraging-trip duration may not always be a reliable index of individual foraging effort.

An earlier study showed that foraging trips made by Gentoo Penguins during chick-rearing, which resulted in capture mainly of fish, had a significantly higher proportion of deeper dives (>54 m) than those that resulted mainly in capture of krill (Croxall et al. 1988a). In our study, most birds took fish (75% by weight; noninstrumented birds) early in the deployment period and krill (95% by weight; both TDR and noninstrumented birds) late in the study period. However, in all three instrumented birds, the proportion of diving time spent in deep dives and, in two birds, mean deep-dive depth increased with time during the deployment period (i.e. fewer and shallower dives were made when fish predominated in the diet). This difference might be due to seasonal variation in the distribution and type of fish prey taken by Gentoo Penguins at South Georgia. The main prey species (*Champsochephalus gunnari* and *Notothenìops larseni*; Croxall et al. 1988a, Williams 1991) spawn in winter (April–June), and younger juveniles inhabit nearshore surface waters. This contrasts with the situation during the summer, when older juveniles and adults occur at greater depth (down to 300 m; Fischer and Hureau 1985).

Comparison of foraging behavior between reproductive and nonreproductive period.—There appears to be little variation in foraging behavior and diving behavior within foraging trips for

Gentoo Penguins at South Georgia between chick-rearing and winter periods (Table 7). First, foraging is almost exclusively diurnal both in summer (Croxall et al. 1988a, Williams et al. 1992) and in winter (this study). In the single case of an instrumented bird remaining at sea overnight, diving activity was greatly reduced during the hours of darkness. Second, although daylength in midwinter is only about one-half that during the chick-rearing period, the absolute duration of the daily foraging trip was the same (i.e. 6-8 h). Thus, Gentoo Penguins spend a greater proportion of available daylength at sea during winter (65-91%) than in summer (42-52%). Third, the estimated foraging range was essentially identical during summer and winter. Fourth, there were no significant differences in the proportion of dive shapes (*U*, *V* and *W*) recorded in summer and winter. Finally, for all characteristics that relate to foraging activity within foraging trips (e.g. dive depth and frequency), summer and winter data are similar (Table 7).

The only significant differences in foraging behavior and ecology of Gentoo Penguins between the reproductive and nonreproductive periods relate to frequency of foraging trips and mass of stomach contents on return (Table 7). Chick-rearing Gentoo Penguins averaged one foraging trip every day (Williams and Rothery 1990), whereas in winter foraging-trip frequency only averaged 0.8 trips/day. This represents a 20% reduction in trip frequency (Mann-Whitney test, $U = 22$, $P < 0.001$ using units [$n = 14$, 12] of equivalent duration for analysis). Average stomach-content weight of Gentoo Penguins feeding on krill in winter was 37% less than that of chick-rearing birds ($F = 3.00$, df = 8 and 40, $P < 0.01$).

We suggest that, when a Gentoo Penguin is at sea, there is very little seasonal variation in the pattern and rate of diving activity. However, if foraging-trip frequency (or total time spent foraging over an extended period) and mass of stomach contents on return ashore are useful indices of foraging effort, nonbreeding Gentoo Penguins actually show reduced foraging effort in winter. This contradicts the hypothesis of diurnal-foraging species increasing their foraging rates during winter in response to decreased daylength (Walsberg 1981), but these differences might simply relate to the absence of dependent offspring in winter. Once the requirement to make daily foraging trips to provision chicks is removed, adults presumably need not forage as regularly or bring as much food ashore. The reduction in foraging-trip frequency in winter also might reflect adults choosing to foraging only when they need to replenish their own body reserves, or adults avoiding days of particularly adverse environmental conditions (including periods of low local food availability).

The lack of variation in the pattern and rate of diving between seasons is similar to the situation found in relation to breeding success in chick-rearing Gentoo Penguins (Williams et al. 1992). Birds that subsequently lost their chick(s) had foraging-trip durations only one-third those of successful birds, but showed no differences in frequency of diving or the proportion of time spent in deep dives. This reinforces our conclusion that foraging effort in Gentoo Penguins is varied by changes in frequency and duration of foraging trips, rather than by changes in the pattern and rate of diving.

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