FORAGING BEHAVIOR OF GENTOO AND CHINSTRAP PENGUINS AS DETERMINED BY NEW RADIOTELEMETRY TECHNIQUES

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ABSTRACT.—Analysis of radio signals from transmitters affixed to 7 Gentoo (*Pygoscelis papua*) and 6 Chinstrap (*P. antarctica*) penguins allowed us to track penguins at sea. Signal characteristics allowed us to distinguish among 5 foraging behaviors: porpoising, underwater swimming, horizontal diving, vertical diving, and resting or bathing. Gentoo Penguins spent a significantly greater portion of their foraging trips engaged in feeding behaviors than Chinstraps, which spent significantly more time traveling. Gentoos had significantly longer feeding dives than Chinstraps (128 s vs. 91 s) and significantly higher dive-pause ratios (3.4 vs. 2.6). These differences in foraging behavior suggest Gentoo and Chinstrap penguins may have different diving abilities and may forage at different depths. *Received 3 June 1985, accepted 24 April 1986.*

THE trophic relationships among *Pygoscelis* penguins, the Adélie (*P. adeliae*), Chinstrap (*P. antarctica*), and Gentoo (*P. papua*), have been a major focal point of research in recent years, particularly with respect to the ecology of their major prey species, krill (*Euphausia superba*). To date, however, our knowledge of the birds' feeding ecology is largely derived from stomach samples obtained ashore (Emison 1968; Croxall and Furse 1980; Croxall and Prince 1980a; Volkman et al. 1980, 1986; Lishman 1985).

Diving depth is one aspect of penguin foraging behavior that has been investigated in some detail. Multiple depth recorders, logging the number of dives within set depth ranges, have been deployed on King (*Aptenodytes patagonica*; Kooyman et al. 1982), Chinstrap (Lishman and Croxall 1983), and Gentoo (Costa pers. comm.) penguins. Maximum diving depths have been reported for Emperor (*A. forsteri*; Kooyman et al. 1971), Black-footed (*Spheniscus demersus*; Wilson and Bain 1984), and Gentoo (Adams and Brown 1983) penguins. Feeding range also has been investigated, but indirectly, using nest relief intervals (Williams and Siegfried 1980, Ainley et al. 1984, Croxall et al. 1984).

We report a new method of tracking penguins at sea that allowed us to differentiate among behaviors during foraging trips. This method improved our understanding of penguin feeding efficiencies, ranges, and traveling speeds, and permitted preliminary comparisons of Gentoo and Chinstrap penguin foraging behaviors.

METHODS

This study was conducted at a breeding rookery at Point Thomas, King George Island, South Shetland Islands, Antarctica (62°10'S, 58°30'W), between 26 January and 12 February 1984. We attached radio transmitters (1.5 cm in diameter, 5 cm long, 25 g) to the backs of 7 Gentoo and 6 Chinstrap penguins rearing chicks. We secured them to back feathers with Devcon epoxy and two plastic tie-wraps. A 30-cm long antenna curved upward from the penguin's back to assure it was well above the water when the penguin surfaced. We triangulated penguins' locations, at 15-min intervals, with radio receivers (164 MHz) from two huts, 200 m above sea level and approximately 3 km apart. We used a null-peak, 4-element double Yagi antenna receiving system. A third receiver was coupled to a strip-chart recorder and continuously monitored a single penguin during its foraging trip. Signals from foraging penguins were received only when the bird was on the surface and the antenna was not submerged. Thus, strip charts provided profiles of the surface vs. underwater time during penguins' foraging trips. Penguins were tracked between 0900 and 2300, and the two species were alternated over the study period. Krill was apparently plentiful in Admiralty Bay during this time as all penguins foraged exclusively in the bay, within 10 km of the rookery.

All data are expressed as means ± standard error.

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Statistical analysis was done using the Mann-Whitney *U*-test or *G*-test with Yates correction.

RESULTS

Foraging behavior patterns.—The foraging track of Gentoo Penguin 3875 and sections from its chart recording are illustrated in Fig. 1. We were able to distinguish several types of diving patterns from the strip-chart records. We believe these indicate different behaviors such as resting at the surface, two modes of traveling (porpoising and underwater swimming), and two feeding behaviors (horizontal and vertical diving). Resting at the surface included time spent bathing.

Porpoising always was used by penguins leaving from or returning to the immediate vicinity of the beach. Outward-bound porpoising often was followed by bathing, and both behaviors were confirmed visually. Rapid porpoising, then bathing, is a constant feature of Adélie Penguin departure at Cape Crozier in the Ross Sea (Ainley 1972). Underwater swimming, the primary method of traveling used by penguins, accounted for 73% of all traveling time. It consisted of dives, averaging 50 s each, followed by surface pauses, averaging 12 s. Horizontal diving behavior followed underwater swimming and preceded vertical diving in 5 of the 6 penguins for which we have complete records. Penguins that exhibit this foraging pattern moved considerable distances by alternating periods of long dives with one or two short dives. The short dives were of approximately the same duration as the dives of underwater swimming. We hypothesize that horizontal diving may be the primary method of searching behavior used by penguins. The long dives of this behavior pattern may be to explore the deeper layers of the water column for krill. When no prey are located, the penguin moves to a new location by short "traveling dives" before diving again to search for prey. Vertical diving, like underwater swimming, was characterized by regular intervals of dive-to-surface pause times. The duration of dives and pauses were significantly longer, however, and the penguins remained in a localized area during vertical diving (Fig. 1).

For analysis of the foraging behavior of the penguins, feeding dives were defined as all dives during vertical diving, plus the long dives during horizontal diving; traveling dives were all underwater swimming dives plus the short dives during horizontal diving behavior. Porpoising was not considered to be diving.

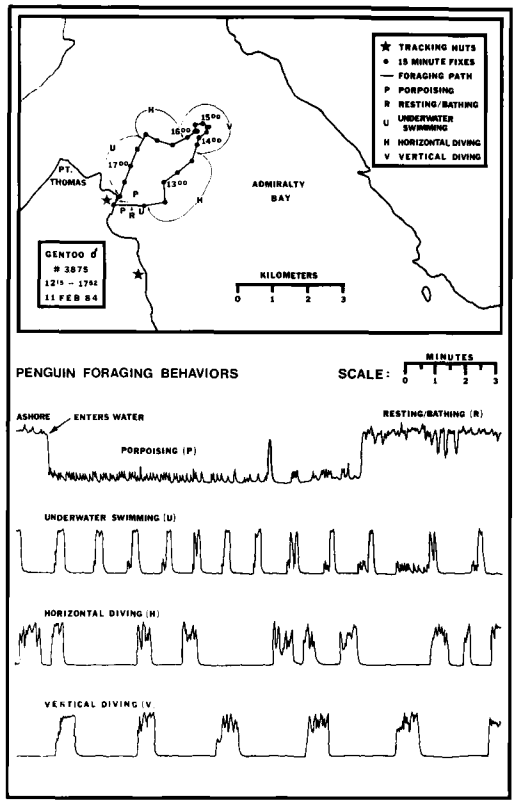

Fig. 1. The foraging trip of Gentoo male 3875 in Admiralty Bay. The penguin's path was plotted from compass bearings triangulated by radio and taken at 15-min intervals from the two tracking huts. Foraging behaviors were copied from a continuous strip chart. Whenever the penguin was submerged, the signal was lost and the strip-chart pen returned to baseline; upon surfacing, the radio signal caused the pen to deflect upward and remain there until the next dive. The ragged look of surface periods during horizontal and vertical diving was caused by changes in the orientation of the antenna because of bird movement and from waves washing over the bobbing penguin, which interfered with the signal's propagation. The paper speed of the strip chart was 16 mm/min. Data on surface times and dive times were taken directly from the charts by converting linear distance to time.

Comparisons of Gentoo and Chinstrap foraging behaviors.—Gentoo Penguins spent a significantly greater portion of foraging trips engaged in feeding behaviors (horizontal and vertical div-

ing) than in traveling behaviors (porpoising and underwater swimming) than did Chinstrap Penguins ($G = 5.47$, $P < 0.025$; Table 1). Gentoos made significantly longer vertical dives than Chinstraps (128 ± 4.5 vs. 91 ± 4.9 s; $U = 42.00$, $P < 0.005$) and had significantly longer maximum dive times (189 ± 8.4 vs. 130 ± 4.3 s; $U = 12.00$, $P < 0.01$; Table 2). Gentoos also had significantly higher dive/pause ratios during vertical diving (3.4 ± 0.2 vs. 2.6 ± 0.2; $U = 36.50$, $P < 0.005$; Table 2). Gentoo Penguins made a mean 193 dives during 6.1 h of foraging, 90 of which (47%) were feeding dives; Chinstraps made 182 dives during 5.3 h, 74 of which (41%) were feeding dives (Table 2).

We calculated traveling speeds for penguins returning from feeding areas to the breeding rookeries. The mean (±SE) traveling speed for 3 Gentoo and 3 Chinstrap penguins was 4.5 ± 0.4 km/h (Table 2). Penguin return trips varied from 20 to 64 min. Strip-chart recordings assured us penguins were traveling (i.e. porpoising or underwater swimming) throughout their returns.

TABLE 1. The percentage of foraging time spent in different behaviors by Gentoo and Chinstrap penguins.[a]

	Foraging trip (h)	Foraging behaviors[b] (%)				
		Traveling		Feeding		
		P	U	H	V	R
Gentoo Penguins[c]						
3894 F	5.7	5	12	53	21	1
UB M	7.1	3	24	6	60	6
3875 M	5.5	6	15	34	44	1
Mean	6.1	5	17	31	44	3
Chinstrap Penguins[c]						
3896 M	4.8	9	18	11	57	4
3963 F	4.4	13	17	22	46	2
3893 F	6.8	10	47	7	32	4
Mean	5.3	11	27	14	45	3

[a] From analyses of strip-chart recordings of complete foraging trips.

[b] P = porpoising, U = underwater swimming, H = horizontal diving, V = vertical diving, R = resting or bathing on surface.

[c] M = male, F = female.

DISCUSSION

Using radiotelemetry to track penguins at sea and to distinguish among their behaviors provided detailed records of the activities of penguins during foraging trips and allowed two important general conclusions. First, a large percentage of dives recorded using multiple depth recorders (MDRs) in some other studies probably are not feeding dives. Therefore, MDRs could overestimate the number of feeding dives and underestimate the foraging efficiencies of penguins. Second, traveling speeds of penguins at sea may be considerably lower than the 7.2 km/h swimming speeds reported for Adélies (Kooyman 1975), and penguin foraging ranges based on these swimming speeds may have been overestimated (Croxall and Prince 1980b, Croxall et al. 1984).

Multiple depth recorders log the number of dives within preset depth ranges. Because Kooyman et al. (1982) deployed MDRs with minimum thresholds of 5 m, their estimates of King Penguin feeding dives probably do not include traveling dives and are likely to reflect feeding effort. Lishman and Croxall (1983), however, had no lower thresholds set on MDRs placed on Chinstrap Penguins, because Chinstraps forage at shallower depths. Our calculations from their histograms show that 445 of 1,110 dives made by Chinstrap Penguins were recorded in the shallowest depth range (0–7 or 0–10 m). This represents 40% of all dives, many of which may have been dives associated with traveling (i.e. porpoising and underwater swimming). Dives during underwater swimming accounted for 44% of all dives by the penguins we studied.

Penguins can swim 7.2 km/h (Kooyman et al. 1971); however, the sustained traveling we observed consisted of an underwater locomotory phase followed by a short pause at the surface (see Fig. 1). Analysis of the dive/pause ratios showed that penguins were swimming during only 76% of the time they were traveling; the remaining time was spent on the surface. Calculating an overall speed by taking 76% of 7.2 km/h results in an estimate of 5.5 km/h. The 4.5 km/h mean returning speeds observed were lower still, perhaps because calculations were based on straight-line distances between feeding and landing areas, whereas penguins swam more erratically.

Comparisons of Gentoo and Chinstrap foraging behaviors provided new insights into their feeding ecology. Gentoo and Chinstrap penguins ate predominantly krill during chick rearing; 3-year means were 86.5% and 99.4% by wet mass of all their food, respectively (Volk-

TABLE 2. Comparisons of Gentoo and Chinstrap penguin foraging behaviors.[a,b]

Bird[c]	Total foraging trip (h)	Total no. dives	Total feeding time (h)	No. feeding dives	Mean dive time (s)	Mean pause time (s)	Dive/pause ratio	Maximum dive time (s)	Travel speed (km/h)
Gentoo Penguins									
3894	5.7	192	4.6	85	131	38	3.5	203	4.2
UB	7.1	231	4.3	92	108	41	2.6	174	5.3
3875	5.5	157	4.3	93	119	34	3.6	190	3.1
2245	—	—	—	—	135	45	3.0	—	—
3895	—	—	—	—	132	30	4.3	—	—
UB	—	—	—	—	128	31	4.1	—	—
2219	—	—	—	—	145	50	2.9	—	—
Mean	6.1	193	4.4	90	128**	39	3.4**	189*	4.2
Chinstrap Penguins									
3896	4.8	139	3.0	86	97	31	3.2	126	4.7
3963	4.4	158	3.3	69	103	47	2.2	139	3.9
3893	6.8	249	3.6	68	99	34	2.9	126	5.7
3885	—	—	—	—	83	33	2.5	—	—
2573	—	—	—	—	71	40	1.8	—	—
2605	—	—	—	—	91	33	2.7	—	—
Mean	5.3	182	3.3	74	91	36	2.6	130	4.8

[a] Data for the first 3 Gentoo and Chinstrap penguins are from entire foraging trips and include a strip-chart record. Dive and pause time data for the remaining penguins were collected by timing a minimum of 10 consecutive dive/pause cycles during vertical feeding.

[b] * = Differs significantly from Chinstrap Penguin; Mann-Whitney *U*-test, $P < 0.01$. ** = $P < 0.005$.

[c] UB = unbanded penguin.

man et al. 1986). Gentoo Penguins require significantly more krill to rear their chicks to fledging than do Chinstrap chicks (118 kg vs. 73 kg per breeding pair; Trivelpiece et al. in press) and have significantly shorter nest relief intervals during chick rearing (12.5 h vs. 16.7 h; Volkman et al. 1986). Foraging ranges based on nest relief intervals, feeding times, and traveling speeds are estimated as within 17 km of the rookery for Gentoos and within 27 km for Chinstraps (Trivelpiece et al. in press). Thus, Gentoos require more krill per day for their chicks, and they acquire this food from a more restricted foraging range. We suggest that Gentoos can do this because of their greater diving abilities.

Gentoos dove significantly longer and had significantly higher dive/pause ratios than did Chinstraps (Table 2). Dive/pause ratios may indicate physiological diving abilities (Dow 1964), which in cormorants (*Phalacrocorax* spp.) are correlated with feeding depths (Stonehouse 1967a, Ainley et al. 1981). Gentoo Penguins have been caught in trammel nets at 100 m depth (Conroy and Twelves 1972) and are known to dive to at least 135 m (Costa pers. comm.); none of 1,110 dives by 4 Chinstrap Penguins exceeded 70 m and only 6% of the dives exceeded 45 m (Lishman and Croxall 1983). A direct relationship between body size and diving depth has been postulated for penguins (Stonehouse 1967b). Consistent with this idea, Gentoo Penguins are the largest of the pygoscelids, with mean adult masses during the chick phase of 5.3 kg, compared with 4.0 kg for adult Chinstraps (Volkman et al. 1980).

In the shallow-water regions of King George Island, krill aggregations occur in a broad layer from 10 to 80 m deep during the night, and descend to a daytime level between an upper 30–60 m limit and a lower 90–120 m limit (Kalinowski and Witek 1980). Thus, whereas the deeper-diving Gentoos can exploit any krill aggregations they locate, Chinstraps may be unable to feed effectively on deep krill swarms and therefore must spend more time traveling in search of available prey.

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