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DIVING PATTERNS IN RELATION TO DIET OF GENTOO AND MACARONI PENGUINS AT SOUTH GEORGIA[1]

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Abstract. The depths attained on 1,444 dives by 14 Gentoo Penguins (*Pygoscelis papua*) and 6,352 dives by eight Macaroni Penguins (*Eudyptes chrysolophus*) were recorded, together with the timing and duration of the foraging trip and the amount and type of prey caught. Macaroni Penguins ate only Antarctic krill *Euphausia superba.* When feeding only at night they made no dives deeper than 20 m; on all-day trips 36% of dives were between 20 to 80 m. Gentoo Penguins fed during the day. When they caught krill, 77% of dives were shallower than 54 m; when fish were taken, 59% of dives were 54 to 136 m, which is consistent with the benthic-demersal habit of the juvenile *Notothenia* and *Champsocephalus* fish they eat. The pattern of predation on krill by both penguin species is consistent with its vertical migration to the surface at night and dispersal through the water column during the day. The food requirements of chick-rearing Macaroni Penguins would be met by catching at least six adult krill per dive (or 150 juvenile krill or amphipods). For similar Gentoo Penguins, a minimum of 15 adult krill per dive (one every 8 sec), or one fish every third dive, is needed. Recorded interannual variations in krill size can treble these rates, which would also be doubled if half the dives were for travelling, not feeding.

Key words: Gentoo Penguin; Macaroni Penguin; Pygoscelis papua; Eudyptes chrysolophus; *Antarctic krill;* Euphausia superba; *fish; diving; diet; foraging; prey capture rate.*

INTRODUCTION

Penguins are the most highly adapted of all birds for life under water. However, little is known about their diving patterns and performance, which are fundamental aspects of their feeding ecology, influencing the prey they encounter and their efficient exploitation of these. Recent reviews of feeding ecology and diving performance in penguins (Croxall and Lishman 1987, Kooyman and Davis 1987) indicate that the depths typically reached during diving by free-living penguins are known for only five species. Only for King Penguins (*Aptenodytes patagonicus*), Chinstrap Penguins (*Pygoscelis antarctica*), and Jackass Penguins (*Spheniscus demersus*) are data other than maximum depth attained available (Kooyman et al. 1982, Lishman and Croxall 1983, Wilson 1985).

In none of these studies was it possible to measure accurately both the time that the birds spent at sea and also the quantity and identity of food caught. In this study we obtained the first data on the diving patterns of Gentoo (*Pygoscelis papua*) and Macaroni (*Eudyptes chrysolophus*) penguins and examine these in relation to foraging trip timing and duration and to the type and amount of food obtained.

Fieldwork was carried out at Bird Island, South Georgia (54°S, 38°W), as part of an extensive study of the feeding ecology and energy budgets of these species (Croxall and Prince 1980a; Davis et al. 1983; Davis, Croxall, and O'Connell, unpubl.), in the austral summers of 1984 to 1985 and 1985 to 1986. Macaroni and Gentoo penguins are the two commonest species of penguin at South Georgia (with breeding populations estimated at about 5,000,000 and 100,000 pairs respectively; Croxall et al. 1984) and they are also abundant at Bird Island (breeding populations of ca. 75,000 and 6,000 pairs respectively;

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Croxall and Prince 1980b). Both species are therefore important consumers of marine resources at South Georgia, Macaroni Penguins being preeminent among avian species (Croxall et al. 1984, Croxall et al. 1985, Croxall and Prince 1987) but there are numerous biological and ecological differences between the two species. In the present context the most important of these are that Gentoo Penguins mainly feed inshore (within 10 km of land; Croxall and Prince 1987; J. L. Bengtson, unpubl. data) and attempt to rear two chicks, which are fed on adult Antarctic krill (*Euphausia superba*) and young stages of mainly benthic-demersal notothenioid fish (Croxall and Prince 1980a, Croxall and Lishman 1987). In contrast, Macaroni Penguins feed mainly offshore, rarely within sight of land, and rear one chick on a diet of both adult and juvenile *E. superba*, fish being very rarely recorded (Croxall and Prince 1980a; Croxall et al., in press).

METHODS

DIVING DEPTH

The depth histogram recorder (DHR) described by Kooyman et al. (1983) was used. In brief, this is cylindrical (95.0 mm long by 23.0 mm diameter) and weighs 95 g (approximately 1.6% of adult Gentoo Penguin and 2.3% of adult male Macaroni Penguin body weight). The DHR contains eight electronic counters which respond to different preset pressure thresholds, each of which is equivalent to a different depth. When the penguin dives below the surface of the water, the increase in pressure with depth is converted to a voltage shift by a pressure transducer in the DHR. If the voltage exceeds the threshold of one or more of the counters, it is recorded in each of them. The setting of these thresholds was checked in the laboratory against a pressure station before and after each deployment. The DHR was attached to feathers in the middle of the back with two small metal hose clips. Each bird was also given a distinctive paint mark (number or symbol) on the breast to facilitate recapture on its return to the colony. Each recorder was used for a single foraging trip only, removed when the bird was recaptured, and the number of dives registered in each counter was read through a decoding processor which was attached to the DHR in the laboratory. Birds were selected after they had fed a chick and when it was judged that they were about to leave the colony to return to sea.

FORAGING TRIP DURATION

When DHRs were being deployed, birds bearing these were watched until they entered the sea and a continuous watch was then maintained during daylight hours until the bird returned. Birds were weighed before and after the foraging trip. In both study seasons the attendance patterns ashore of a sample (n = 10 to 15 birds originally) of breeding birds of each species was recorded continuously throughout most of the chick-rearing period using radio transmitters and automatic recording apparatus. The radio transmitters (15 mm diameter, 50 mm length, 25 g weight) were attached to the penguins' back feathers with epoxy resin and hose clamps or plastic tie wraps. To record the presence of these birds at the colony a Yagi 4-element antenna was mounted on the roof of a small wooden blind and connected to a radio receiver (164 MHz) inside, set to scan continuously in sequence the frequencies of the deployed transmitters for 10 sec each. The receiver was connected to a strip chart recorder. This system provided control data against which the foraging trip durations of the experimental birds could be compared. It also confirmed that penguins do not arrive ashore at the breeding colony during the night. Data on the foraging-attendance patterns during postbrooding chick-rearing of paint-marked birds (Croxall, unpubl. data), whose presence was recorded on three to four visits (of 1 hr each) daily, are consistent with those of birds with radios. Thus paint-marked Gentoo Penguins spent about 12 hr at sea (range = 6 to 24 hr; n = 210) and Macaroni Penguins either 12 hr (range = 10–16 hr; n = 140) or 24 hr (range = 18–50 hr; n = 72).

FOOD

The contents of the stomachs of experimental birds returning ashore were collected using stomach lavage techniques (Wilson 1984). Birds were flushed repeatedly until no more food was obtained; we have confirmed that this corresponds to an empty stomach. In 1985 five complete stomach samples and in 1986 10 such samples were obtained weekly from both species throughout the chick-rearing period. These samples enabled us to check that experimental birds were taking broadly similar prey and had a similar mass of food in the stomach to other individuals engaged in similar parental duties at the same stage of the chick-rearing period. For control birds in both seasons and for experimental birds in

1986, complete stomach contents were weighed fresh at the time of collection and sorted on the same day. Krill (and other crustaceans), fish and squid were sorted, weighed, and preserved in 10% formalin. Both sagittal otoliths were removed from intact fish crania and these, together with any loose otoliths, counted and stored dry in plastic tubes. All material was then returned to the United Kingdom for further processing. All krill in samples were counted, including specimens represented only by pairs of eyes. A sample of 100 krill from each stomach was measured, either the straightened standard length of perfectly intact specimens or the carapace length of damaged ones and sex and reproductive status was recorded for as many specimens as possible. Fish otoliths were identified to as low a taxonomic category as possible, length, breadth, and thickness measured (to 0.01 mm) and weighed (to 0.001 g). These measurements were used in regression equations to estimate the standard length and weight of the original fish specimens (using principally data from Hecht [1987] and unpublished BAS data). Digestion of otoliths was not a problem in this study because 90% of otoliths were removed from intact fish crania.

RESULTS

In 1985 eight deployments of DHRs were made on Gentoo Penguins during the chick-rearing period. Dietary data and foraging trip duration were only recorded for four of these. Six deployments were made on sexed adults at a similar stage in the breeding cycle in 1986. All deployments on Macaroni Penguins were made on male birds (because of concern that the DHR might be too large a package for the female, which is 20% smaller than the male) in 1986. Six records were obtained during late chick rearing and two from birds during the extended trip to sea between chicks fledging and the return of adults to the breeding colony to commence molt (referred to here as the premolt period). One of these two devices was only retrieved after molt had finished and therefore the duration of the foraging trip was unknown. Neither of these birds was lavaged but krill was the sole food of nonexperimental birds at this time.

Macaroni Penguins ate krill almost exclusively (94% by weight of diet) in 1986; all were adults, averaging 52 mm long (range = 31–62 mm; n = 4,600). Their only other prey were fingerlings of the fish *Notothenia rossii* (20 to 30 mm long; 4% by weight) and amphipods *Themisto gaudichaudii* (ca. 20 mm long; 2% by weight). Gentoo Penguins ate either krill (91% by weight, occasionally with one or two fish present) or fish (87% by weight, usually with a few krill). Amphipods (*T. gaudichaudii*) were present as a trace in a few samples. The fish were mainly Antarctic cod (*Notothenia rossii* and *N. neglecta*) or ice fish (*Champsocephalus gunnari*), in roughly equal proportions. A few lantern fish Myctophidae were present in 1985 to 1986. The *Notothenia* were mainly juveniles (a few subadults) from 14 to 42 cm in estimated length, equivalent to weights of 27 to 1,170 g (mean ca. 130 g). The *Champsocephalus* were smaller, 16 to 20 cm in length, 16 to 34 g (mean 22 g) in weight. Krill were all adults; they averaged 52 mm (range = 35–64 mm; n = 3,400) length in 1986 but only 37 mm (range = 28–60 mm; n = 500) in 1985.

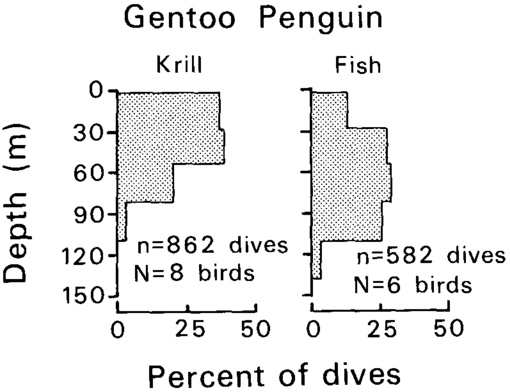

FIGURE 1. Dive depth histograms (proportion of dives terminating in each stratum) for Gentoo Penguins feeding on fish and krill.

The diet of the four 1985 Gentoo Penguins for which it was unknown has been assigned on the basis of the statistically significant similarity between their diving patterns and those of birds whose diet was known. We feel that this is also biologically realistic because of over 100 Gentoo Penguin complete-stomach samples, fewer than 10% contained significant quantities of both fish and krill. Excluding these four birds changes none of the interpretations below. Diving data are presented in detail in Appendix I.

For the 1986 Gentoo Penguins, there were no significant differences between males and females, either in the composition of the diet, timing, and duration of foraging trip or in any diving parameter. The important data from both sea-

TABLE 1. Diving data ($\bar{x}$ ± SD, range beneath) for Gentoo Penguins.

Diet	n	Trip duration (hr)	No. of dives/trip	No. of dives/hr	Depth reached (%) <54 m	Depth reached (%) >54 m
Fish	6	11.3 ± 1.7	97.0 ± 26.2 (57–123)	9.8 ± 1.1	41	59
Krill	8	10.7 ± 1.3	107.8 ± 31.0 (69–169)	9.3 ± 2.5	77	23

sons are summarized in Table 1 in relation to the highly significant differences in dive depth distribution of birds which had been eating fish and krill (Fig. 1). In essence, foraging trips that resulted in capture mainly of fish included a significantly higher proportion of deeper dives (i.e., to >54 m) than those which resulted in the capture of mainly krill ($\chi^2 = 161$; $P < 0.001$). There were no associated significant differences in trip duration or number and frequency of dives. Foraging trip duration was longer, but not significantly so ($t = 0.47$; $P > 0.1$), than trips made by birds without DHRs (9.8 ± 2.7 hr, $n = 128$). All but two of the foraging trips of instrumented Gentoo Penguins were completed during daylight hours. The two exceptions were the trip with the most dives (169), whose exact duration was not recorded (it was between 12 and 16 hr) and the longest (12.1 hr) of the trips made by birds which caught krill. Neither dive profile was anomalous.

For Macaroni Penguins (Table 2) the main differences in dive depth distribution (Fig. 2) and other parameters relate to the duration of the foraging trip. Thus birds that were away from the colony only overnight (12-hr trips, including 7 to 8 hr of darkness) made significantly fewer dives in total, but more per hour, than birds in either of the other categories and made no dives exceeding the shallowest depth threshold (20 m). In contrast, all birds which spent a complete day or more at sea averaged 45% (range = 31–54%) dives to depths greater than 20 m. The depth histograms of premolt birds and of chick-rearing birds in this latter category are not significantly different; other comparisons are difficult because the duration of the foraging trip by the second premolt bird was unknown. The single bird with full data might appear to have made relatively fewer dives per hour than the chick-rearing birds. However, if the other premolt bird, which made 3,374 dives, had been absent for the mean duration of the premolt period at sea (14 days) then it would have averaged 10 dives per hour, very similar to the values for chick-rearing birds.

The foraging trip durations of chick-rearing birds without DHRs (i.e., either with radios or individual marks) are complex (Croxall, unpubl. data). In brief, during the brooding period only females forage, delivering meals daily as a result of trips almost equally divided between 12 hr and 24 hr duration, the frequency of longer trips increasing as the chick grows. During the early crèche period females continue this routine; males bring meals to the chick every 2 to 3 days. Thereafter (and corresponding to the main study period here) both sexes share duties approximately equally and trip durations have three modes, of ca. 12 hr, 24 hr, and 48 hr with a few (<5%) lasting 48 to 72 hr. Consequently we have no evidence that birds with recorders make longer trips than those without.

TABLE 2. Diving data ($\bar{x}$ ± SD; range beneath) for Macaroni Penguins.

Status	Time	n	Trip duration (hr)	No. of dives/trip	No. of dives/hr	Depth reached (%) <20 m	Depth reached (%) >20 m
Chick rearing	Night	3	12.6 ± 0.9	203 ± 14 (190–218)	16.1 ± 0.1	100	0
	Night and day	3	40.0 ± 28.1	392 ± 247 (243–677)	10.1 ± 0.8	56	44
Premolt	Night and day	2	264	1,195–3,374	4.5	54	46

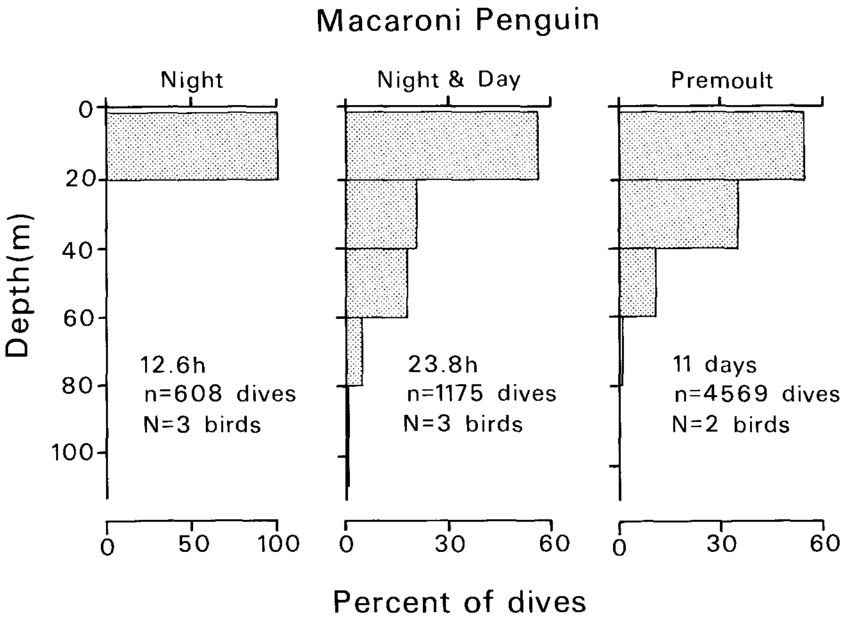

FIGURE 2. Dive depth histograms for Macaroni Penguins on foraging trips at night, for a complete day during chick rearing and during the premolt period.

DISCUSSION

EFFECT OF INSTRUMENT

Although DHRs weigh less than 3% of the mass of the experimental penguins, they are relatively bulky and, considering the highly streamlined nature of penguins (Nachtigall and Bilo 1980), likely to cause drag. Wilson et al. (1986) tried to estimate the importance of this effect on Jackass Penguins. They found that travelling speed, y (m sec^{-1}) was related to device cross-sectional area, expressed as a percentage of penguin cross-sectional area, x, by the equation $y = 2.14 - 0.063x$, with device size explaining about half the variance in mean speed. With our DHRs, the cross-sectional area (415 mm^2) is about 3% of the cross-sectional area of a male Macaroni Penguin (ca. 14,000 mm^2). This would represent a 9% reduction in travelling speed. For the larger Gentoo Penguins speed reduction would only be about 5 to 6%. The devices that Wilson et al. (1986) used in their experiments, however, were not streamlined. DHRs are tapered anteriorly, which should help reduce drag. Wilson et al. (1986) found no significant difference in the energy consumption of Jackass Penguins with and without devices but noted that the mass of prey delivered to the chicks was proportional to the distance travelled. In our case (Table 3) the mass of prey brought ashore was not significantly different between instrumented and control birds, nor were the durations of foraging trips significantly different (although this would not be easy to detect with Macaroni Penguins) but we cannot exclude the possibility that instrumented birds used more energy.

DIVE DEPTH AND PATTERN

There is no previous published information on Macaroni Penguin diving. The difference between the dive pattern from night and night-and-day trips suggests that they rarely dive below 20 m at night and that the 36% of dives terminating below 20 m are probably made during the day. This would be consistent with Macaroni Penguins exploiting the natural vertical migration of Antarctic krill (virtually their exclusive prey at South Georgia), which rise towards the surface at night and sink during the day (Kalinowski and Witek 1980, Everson 1982). The same suggestion was made to account for the very similar diel changes in diving patterns (but based on continuous records) of Antarctic fur seals (*Arctoceph-*

TABLE 3. Comparisons between penguins with dive recorders (DHR) and those without (controls). Values are $\bar{x}$ ± SD, with sample size in parentheses.

	Gentoo Penguin				Macaroni Penguin	
	DHR		Control		DHR	Control
Foraging trip duration (hr)	11.0 ± 1.5 (9)		9.8 ± 2.7 (128)		12.6 ± 0.9 (3) 40.0 ± 28.1 (3)	11.8 ± 2.1 (130) 28.2 ± 5.5 (52)
Stomach content mass (g)	801 ± 251 (10)		878 ± 262 (40)		408 ± 210 (6)	448 ± 259 (40)
Diet composition[a] (% by wt)	K	F	K	F		
Krill	92	15	89.8	13.1	95	93.5
Fish	8	85	10.2	86.9	3	5.0
Other			0.1	0.1	2	1.5
n	(6)	(4)	(28)	(12)	(6)	(40)

[a] K: samples containing mainly krill; F: samples containing mainly fish.

alus gazella) from Bird Island, South Georgia (Croxall et al. 1985a).

For Gentoo Penguins the range of diving depths recorded here encompasses the few previous data. Thus Conroy and Twelves (1972) captured a Gentoo Penguin at Signy Island, South Orkney Islands at 100 m in a trammel net. Adams and Brown (1983) used capillary tubes to record the maximum depth attained over one or more foraging trips at Marion Island. Of 19 birds, 16 did not exceed 20 m, two attained 40 m, and one bird exceeded 70 m. This is rather different from our results where all exceeded 20 m and five, eight, and one bird respectively exceeded 54 m, 81 m, and 109 m. We cannot explain why Marion Island birds appear to make shallower dives than South Georgia ones; there is no obvious difference in the inshore water depths around the islands, the 100-m contour generally being within 1 km or so of both sites.

Gentoo Penguins which mainly catch krill tend to have rather few other prey in their stomachs (Table 3). Because all but two of the experimental birds were foraging only during the day, and krill tends to be away from the surface at this time, it is not surprising that most dives (63.2%) terminate below 28 m. If anything, our data will underestimate the proportion of feeding dives to greater depths, because any travelling dives are certain to be shallower than 28 m.

Gentoo Penguins taking fish usually also have some krill present. If catching these krill (and any travelling dives) accounts for most of the 41% of dives shallower than 54 m (and 77% of dives by krill-catching birds do not exceed this depth) then fish are probably mainly caught on the dives terminating between 54 and 109 m. The main fish prey in both years were juvenile Antarctic cod (*Notothenia rossii* and *N. neglecta*) and juvenile ice fish (*Champsocephalus gunnari*), in roughly equal proportions. Such fish are usually benthic, sometimes benthic-demersal, and live mainly in the seaweed (kelp) beds fringing the coast (Kock 1981, Burchett et al. 1983). We do not know the depths of water in which these fish typically live around Bird Island. The steeply

TABLE 4. Daily food and prey consumption of Gentoo and Macaroni penguins at South Georgia.

				Daily requirements					
					Food (g)[c]				
Species	Activity	Food	FMR[a] (W·kg^{-1})	Energy (kJ)[b]	Adult		Chick		Total
Gentoo	Chick rearing	Krill	7.4	3,708	1,008	+	880	=	1,888
		Fish	7.4	3,708	976	+	880	=	1,856
Macaroni	Chick rearing[f]	Krill	12.1	4,077	1,108	+	450	=	1,558
Macaroni	Premolt	Krill	20.1	7,294	1,982				

[a] Field metabolic rate, from Davis, Croxall, and O'Connell, unpubl.

[b] Calorific content of krill = 4.6 kJ g^{-1} w.w. (Clarke 1984); for fish = 4.75 kJ g^{-1} (average of 4.08 kJ g^{-1} for *Notothenia neglecta* (Crawford 1972) and 5.4 kJ g^{-1} for *N. magellanica* (Hecht and Cooper 1986).

[c] Assimilation efficiency 0.75 (Davis, unpubl. data); food for chicks based on mean weight of stomach contents brought ashore by adults in 1985 to 1986.

[d] Krill averaged 52.4 mm long in 1986; 37.0 mm long in 1985; fish average weight estimated (from otolith data) as 74 g.

[e] Mean with range in parentheses.

[f] Average of the five birds that made trips lasting ca. 12 hr and ca. 24 hr.

shelving topography and proximity to shore of the 100-m depth contour are consistent with the penguin dive data, given the habits of the fish they are exploiting. Some of these fish probably also make vertical migrations, tracking the planktonic elements of their diet, otherwise differences in dive profile between krill and fish-eating birds would probably be accentuated.

DIVE FREQUENCY

Overall the Gentoo Penguins averaged 103 dives per day (range = 57–169, n = 14) and 10.9 (range = 8.8–13.1, n = 9) dives per hour at sea. The three birds radio-tracked by Trivelpiece et al. (1986) at Admiralty Bay, King George Island, South Shetland Islands, were estimated to have averaged 193 (range = 157–231) dives per trip and 31.7 (range = 28.5–33.7) dives per hour at sea, on trips lasting 6.1 hr (range = 5.5–7.1 hr). Some of the differences between these two sets of results may be attributable to the different methods and locations of the two studies. We set our DHR upper threshold at a pressure corresponding to 2 m depth in order to avoid counting submersions during porpoising, which might attain 1 m depth, as dives. We would, therefore, have missed any very shallow dives, but it is inconceivable that these could have represented nearly half the total number of dives. The foraging trips of Gentoo Penguins in Admiralty Bay during the Trivelpiece et al. (1986) study averaged only 60% of the duration of those at Bird Island, which, given the larger number of dives by the Admiralty Bay birds, accounts for the nearly three-fold higher dive frequency. The foraging trip durations of the three experimental birds, however, were very short compared with other data recorded for the same species at the same site, where foraging trips averaging 11.7 and 13.1 hr (as at Bird Island) were reported in two different seasons by Trivelpiece et al. (1987). These and other differences cannot readily be explained but sample sizes are small and there are considerable topographic and hydrographic differences between the shallow, land-locked waters of Admiralty Bay at 62°S and the relatively steeply shelving, open sea surrounding Bird Island at 54°S.

TABLE 4. Extended.

Daily requirements			
No. of prey[d]		Prey per dive[e]	
1986	1985	1986	1985
1,600	5,244	15 (9–23)	49 (31–76)
25		0.3 (0.2–0.4)	
1,320	3,667	6 (5–7)	17 (14–19)
1,680	5,506	15	51

PREY CONSUMPTION AND CAPTURE RATES

We can make a rough estimate of potential prey capture rates by combining estimates of the daily food requirement of adults (and their chicks where appropriate) at the relevant stage of the breeding cycle with information on the average size of prey captured. The results (Table 4) indicate that the food requirements of the various categories of birds that we used are not greatly different (range = 1,558–1,982 g). The number of prey that this represents and hence the average number of prey that would need to be caught per dive, depends critically on prey size. Thus when Gentoo Penguins take fish they need to catch only about 25 to satisfy their daily requirement and this could be attained by capturing one fish on one-third of all dives. When feeding on krill, however, several individuals, on average, have to be caught on every dive. Furthermore, changes in krill standard length are accompanied by substantial changes in body mass. Thus the 15-mm reduction in the mean length of krill caught by penguins in 1985 and 1986 is accompanied by a change in mean mass from 1.18 to 0.36 g and a consequent tripling of the number of prey required. Macaroni Penguins at South Georgia occasionally take significant quantities of *Thysanoessa macrura,* a euphausiid crustacean of mean length 20 mm and of the amphipod *Themisto gaudichaudii* of similar size. Such individuals weigh only about 0.1 g and Macaroni Penguins would therefore need to catch ca. 15,000 prey per day during chick rearing and 20,000 per day during the premolt period. This is equivalent to 150 to 200 individuals per dive.

All these very rough calculations, in addition to assuming that prey are caught on all dives, also assume that all the dives we recorded were feeding dives. Trivelpiece et al.'s (1986) analysis of penguin foraging distinguished three types of dives (as represented by periods of lack of radio signal, presumably when the penguins were below the water surface) according to the length of time the birds spend below the surface (or, more precisely, were unable to transmit a receivable signal) and the interval before the next dive. Underwater swimming, consisting of 50-sec dives followed by 12-sec surface periods, was taken to be the main travelling mode and distinguished from searching behavior (alternating periods of long dives with one or more short ones) and stationary diving (a consistent ratio of subsurface to surface periods, the bird usually moving in a restricted area). If South Georgia birds behave like Admiralty Bay birds, then we would have recorded the subsurface periods during underwater swimming as dives. Such dives comprise 44% of all dives in Trivelpiece et al.'s (1986) study. Therefore only just over half the dives we recorded might represent opportunities for prey capture. This would nearly double the required prey capture rates given in Table 3, with mean values of 27 and 87 per dive for chick-rearing Gentoo Penguins and 11 and 29 and 28 and 90 per dive for chick-rearing and premolt Macaroni Penguins respectively. If the average dive for Gentoo Penguins lasts 128 sec (Trivelpiece et al. 1986), then one krill needs to be caught on average each 1.5 to 5.0 sec during each dive.

The limited data from watching penguins feed in shallow water and in aquaria suggest that they typically catch prey individually and ingest small prey with no visible pause in their swimming (Croxall, pers. observ.). Providing, therefore, that krill are sufficiently aggregated, such prey capture rates should not be difficult to achieve. For Macaroni Penguins feeding on *Thysanoessa* and *Themisto* however, prey capture rates of two to three per second would be necessary. Macaroni Penguin bills, however, are a very different shape from Gentoo Penguins, being much shorter, broader, and deeper and it is possible that this facilitates capture of several small prey at a time. It is notable that while some Macaroni Penguin stomachs may contain large numbers of *Thysanoessa* or *Themisto,* such prey are rarely observed in Gentoo Penguin stomachs and never in large numbers.

COMPARISON WITH OTHER ANTARCTIC SPECIES

Dive depth histograms, obtained from the same type of DHR, are available for King Penguins (which eat fish and squid but not krill or other crustaceans) at South Georgia (Kooyman et al. 1982) and Chinstrap Penguins (which eat only krill) at Signy Island, South Orkney Islands (Lishman and Croxall 1983) and can be constructed from the continuous records of diving activity for female Antarctic fur seals (eating only krill) at South Georgia (Croxall et al. 1985a, Kooyman et al. 1986). These are summarized (Fig. 3) so as to allow comparison with the Gentoo and Macaroni penguin data. This shows a broadly consistent pattern among the krill-eating species, with shallower dives at night than during the day and, overall, shallower dives than when fish prey are sought. The King Penguin stands apart by virtue of its very deep dives but the fact that half the dives of this 12-kg bird are shallower than 50 m is perhaps equally noteworthy. Its main squid prey at South Georgia is *Martialia hyadesi* (formerly identified as *Todarodes*; Croxall and Lishman 1987) which, although regarded as a mesopelagic species, is commonly caught at the surface by albatrosses (Prince 1980, Prince and Morgan 1987). Fish may be more important in its diet than squid and recent studies in the Indian Ocean (Adams and Klages 1987) showed that lantern fish predominate. The species involved (of the genera *Krefftichthys* and *Electrona*) are essentially mesopelagic but occur at the surface at night. The long, 4- to 6-day foraging trips of King Penguins presumably result in a dive frequency distribution comprising shallow dives at night and deeper daytime ones.

The Gentoo Penguin is the only species studied which has a mixed diet involving fish and krill. We do not know why individual birds tend to catch either krill or fish, rather than a mixture. The habit is not confined to South Georgia, because of 46 birds examined at the South Shetland Islands, 76% contained only krill, 15% only fish, and the rest a mixture (Jablonski 1985). This study also showed that the same individual did not catch the same type of prey in successive seasons but some degree of specialization within a season cannot be ruled out. Data on overall diet composition (Croxall and Prince 1980a, Volkman et al. 1980, Jablonski 1985) all indicate that krill are the main prey (at least in the Scotia Sea), the 32% contribution of fish at South Georgia being the highest recorded. Therefore, despite fish being theoretically more economical prey (larger than krill, fewer need to be caught), the greater abundance of krill and its swarming habit presumably result in its being more often encountered and more easily caught than the

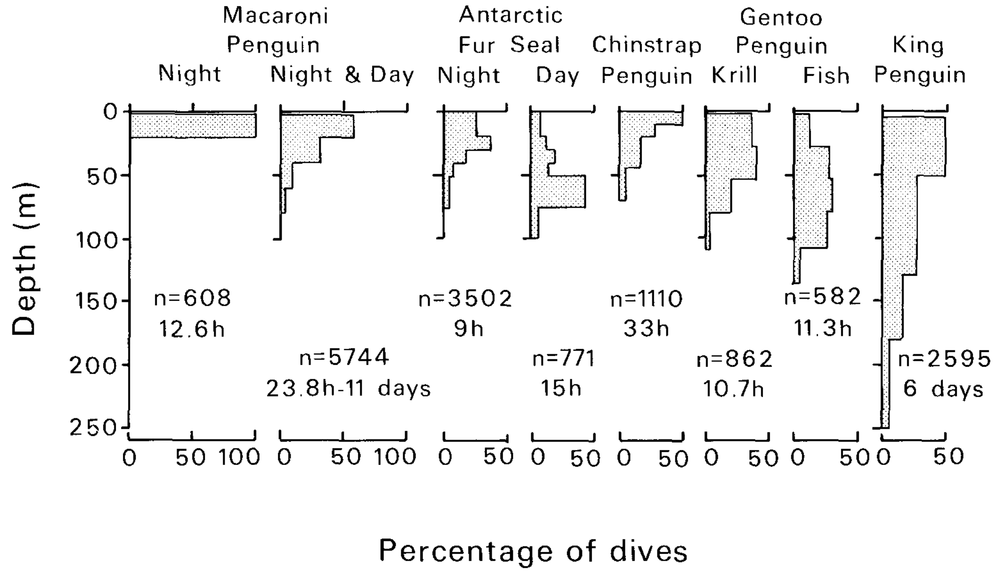

FIGURE 3. Dive depth histograms for Macaroni, Gentoo, King, and Chinstrap penguins and Antarctic fur seals. Sample sizes refer to number of dives; trip durations are mean values.

scarcer, deeper-dwelling fish. It may be that only when krill are not readily encountered do birds make deeper dives to look for fish. These also seem mainly to be exploited when in shoals, because *Notothenia* and *Champsocephalus* are rarely found mixed together in Gentoo Penguin stomachs.

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APPENDIX 1. Number of dives terminating in each depth stratum, diet, and trip duration of Gentoo and Macaroni penguins at South Georgia.

	Gentoo Penguin													
Year	85	85	85	85	85	85	85	85	86	86	86	86	86	86
Sex	—	—	—	—	—	—	—	—	M	F	F	M	M	M
Trip duration (hr)	—	—	—	9.7	—	—	8.8	11.6	13.1	11.2	10.8	12.1	9.4	11.2
Diet[a]	(F)	(F)	F	F	(K)	(K)	K	K	F	F	K	K	K	K
Depth (m)														
2–28	15	23	5	1	48	20	14	19	18	15	49	55	70	42
29–54	23	5	13	27	65	49	25	40	47	46	52	40	41	31
55–81	22	11	11	11	38	38	43	10	54	60	13	18	9	6
82–109	51	43	28	24	18	4	5		3	2				
110–136				24										
136+														
Total	111	82	57	87	169	111	87	69	122	123	114	113	120	79

[a] F: fish; K: krill; parentheses indicate diet assumed (see text).

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APPENDIX 1. Extended.

	Macaroni Penguin							
	86	86	86	86	86	86	86	86
	M	M	M	M	M	M	M	M
	12.5	13.5	11.8	24.0	23.5	72.5	264	?
	K	K	K	K	K	K	(K)	(K)
Depth (m)								
2–20	200	218	190	127	117	467	611	1,934
21–40				56	60	117	446	1,079
41–60				48	57	71	129	349
61–80				12	20	21	9	12
81–100					1	1		
100+								
	200	218	190	243	255	677	1,195	3,374