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DIETS OF PYGOSCELID PENGUINS AT KING GEORGE ISLAND, ANTARCTICA

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ABSTRACT.—The species composition and characteristics of prey consumed by sympatrically breeding Adélie, Chinstrap, and Gentoo penguins were determined by analysis of whole stomachs collected at Point Thomas, King George Island, South Shetland Islands, Antarctica (62°10′S, 58°30′W) during the 1977–1978 breeding season. All three penguins consumed primarily one species of euphausiid, *Euphausia superba*, although Gentoo Penguins ate significantly more fish, *Pleurogramma antarcticum*, than either Adélie or Chinstrap penguins. *E. crystallorophias*, and pelagic and benthic species of amphipods were minor components of the pygoscelid diet. The penguins differed in euphausiid size and in the ratios of male, female, and adolescent euphausiids eaten. These differences were consistent over the entire reproductive cycle. In addition, the species differed in the wet weight of fish consumed by Gentoo Penguins, and in the length of euphausiids consumed by Adélie Penguins. We suggest that these differences in diets are due, in part, to geographical and temporal differences in feeding areas and habitats.

The breeding ranges of the pygoscelid penguins, the Adélie (*Pygoscelis adeliae*), the Chinstrap (*P. antarctica*), and the Gentoo (*P. papua*) overlap in the area of the Antarctic Peninsula, and the birds breed sympatrically at several locations. Whether or not they compete for certain resources (e.g., food and nesting habitat) has recently been much discussed (Conroy et al. 1975a, b, White and Conroy 1975, Trivelpiece and Volkman 1979, Volkman and Trivelpiece, in press). The diets of pygoscelid penguins consist of euphausiid crustaceans, mainly *Euphausia superba*, shoaling fishes, and amphipods (Conroy et al. 1975a, b, White and Conroy 1975, Croxall and Furse 1980, Croxall and Prince 1980). Although White and Conroy (1975) proposed that sympatric pygoscelids consume different prey species and/or prey of different size classes, data to support their hypothesis are limited.

In order to further examine the feeding ecology of this genus, during the austral summer of 1977–1978, we collected whole stomachs from Adélie, Chinstrap, and Gentoo penguins. We wished to quantify the type, abundance and characteristics (e.g., sex, age class, etc.) of the prey species selected by each of the pygoscelids, and to examine any seasonal variation in these measurements.

METHODS

This study was conducted at Point Thomas, King George Island, South Shetland Islands, Antarctica (62°10′S, 58°30′W) from 1 November 1977 to 21 February 1978. All three pygoscelid penguins breed in two rookeries (after Penney 1968) at Point Thomas. The rookeries are separated by a glacial tongue, and are about 3 km apart. An estimated 7,000 Adélie, 290 Chinstrap, and 1,900 Gentoo pairs breed in the East rookery; 11,000 Adélie, 750 Chinstrap, and 700 Gentoo pairs breed in the West rookery. The Polish Academy of Sciences Antarctic Station, Henryk Arctowski, is located 1 km south of the West rookery.

Emison's (1968) technique for pumping the stomachs of Adélie Penguins by orally inserting a hollow plexiglass tube was inapplicable to our study. Samples collected by stomach pumping and compared with contents of complete stomachs taken from the same bird revealed significant differences. Many organisms in whole stomach samples measured 40 to 50 mm, while those in pumped samples were 20 to 35 mm long. Larger krill apparently did not fit in the tube, or were broken during collection. In addition, because different prey species occurred in distinct layers in the stomachs, pumped samples were not always representative of the type of prey species present. The discrepancies between samples collected with stomach tubes, and those from whole stomachs necessitated the use of the latter method in this study. We first used a stomach tube, however, to ensure that only penguins with stomach contents would be killed.

Complete stomach samples were collected from 48 adult Adélie (26 males, 22 females), 29 adult Chinstrap (14 males, 15 females), and 46 adult Gentoo (24 males, 22 females) penguins during the course of the breeding cycle. Penguins with highly vascularized brood patches were caught and killed only in the East rook-

TABLE 1. Composition of pygoscelid stomach contents by wet weight.

	Prey type		
	Euphausiids (%)	Fish (%)	Amphipods (%)
Adélie Penguin*	99.6	0.1	0.3[a]
Chinstrap Penguin*	99.6	0.3	0.1[b]
Gentoo Penguin	84.5	15.4	0.1[c]

* Significantly different from Gentoo ($P < 0.005$, χ^2 test).
Amphipods found in stomachs (see Jazkzewski, in press):
[a] *Cheirimedon, Cyphocaris, Cyllopus, Eurymera, Eusirus, Hyperia, Parathemisto.*
[b] *Cyllopus, Eusirus, Hyperia, Parathemisto.*
[c] *Djerboa, Eusirus, Eurymera, Hyperia, Oradarea, Waldeckia, Pontogeneiella.*

ery (to avoid interfering with on-going studies in the West rookery) as they returned from sea. Birds were killed either by pithing, or by injecting 0.2 ml of sodium pentathol into the spinal cord; death was instantaneous. After the contents of the esophagus and the stomach were removed, penguins were sexed by examination of the reproductive tract, weighed, and the total body length (tip of bill to end of pygostyle), culmen length, and the culmen depth at the nares were measured.

Data collected from whole stomach samples included the weight of the total sample, the weight of the fresh, recognizable euphausiids, fishes and amphipods, and the weight of semi-digested contents. The number of euphausiids consumed per penguin was estimated by calculating the number per gram in a sample of 50 fresh euphausiids from each stomach. This figure was then multiplied by the total wet weight of euphausiids in the stomach. The number of amphipods consumed was determined by direct counts, and fish numbers by counts of intact specimens and/or rostra and eye lenses. Finally, the species, sex, age-class and length (measured from eyes to telson) of 50 individual euphausiids taken randomly from the fresh portion of sach sample were determined. The species and length of all amphipods and intact fish were recorded.

RESULTS

Two species of euphausiids, *Euphausia superba* and *E. crystallorophias,* one species of fish, *Pleurogramma antarcticum,* and several genera of benthic and pelagic amphipods (see Table 1) were found in the penguin stomachs. The diet of Adélie and Chinstrap penguins consisted of nearly 100% krill (*E. superba*) by both wet weight and number of prey items (Tables 1 and 2). The Gentoo Penguin diet was also largely krill, but contained significantly more fish by weight (15.4%) than the other pygoscelids (Table 1). Fish were found in 13% of Adélie, 21% of Chinstrap, and 40% of Gentoo penguin stomachs, however, many were so digested that they could not be identified. Only nine intact fish were found (range, 100 to 250 mm) and these were all from Gentoo Penguin stomachs. Amphipods constituted a minor fraction (<2%) of the diet of all three penguins, and ranged in size from 10 to 54 mm ($\bar{x}$ = 19.8) for Adélies, 17 to 55 mm ($\bar{x}$ = 25.0) for Chinstraps, and 12 to 57 mm ($\bar{x}$ = 21.6) for Gentoos. Occasional nematodes, marine algal fragments, stones, feathers, and mollusc shell fragments were also found, but were not considered to be food items.

TABLE 2. Composition of pygoscelid stomach contents by number.

	Prey type		
Species	Euphausiids (%)	Fish (%)	Amphipods (%)
Adélie Penguin	99.7	0.1	0.2
Chinstrap Penguin	99.8	0.1	0.1
Gentoo Penguin	98.4	1.5	0.1

TABLE 3. Percentages of fresh and semi-digested euphausiids in pygoscelid penguin stomachs.

Species	Fresh (%)	Semi-digested (%)
Adélie Penguin*	35.6	64.4
Chinstrap Penguin*	43.7	56.3
Gentoo Penguin	62.8	37.2

* Significantly different from Gentoo ($P < 0.005$, χ^2 test).

The characteristics of 5,250 sexually mature and adolescent euphausiids were examined. Adélie and Chinstrap penguins consumed 98.4% and 99.8% *E. superba,* and 1.6% and 0.2% *E. crystallorophias,* respectively. Gentoo Penguins consumed only *E. superba.* Although the size ranges of euphausiids eaten by Adélie (10 to 57 mm), Chinstrap (11 to 55 mm), and Gentoo (26 to 55 mm) penguins were similar (Fig. 1), Gentoo Penguins ate larger krill ($\bar{x}$ = 44.7 ± 0.1 mm SE) than did Chinstrap Penguins (42.3 ± 0.2 mm), which in turn ate larger ones than Adélie Penguins (40.6 ± 0.2 mm; $F = 107.230$, df = 2, 5249; $P < 0.005$). All three species consumed greater than 90% sexually mature euphausiids in the 31 to 55 mm range.

The mean weights of Adélie (350 g), Chinstrap (363 g), and Gentoo (432 g) penguin stomach contents did not differ statistically; however, Gentoo stomachs contained greater percentages of fresh food than did those of either Adélie or Chinstrap ($\chi^2 = 15.647$, df = 2, $P < 0.005$; Table 3). Interspecific differences also occurred in the ratio of male, female and adolescent euphausiids consumed by each penguin species (Table 4). These differences were primarily due to the many juvenile euphausiids eaten by Adélies, and the large percentage of male euphausiids consumed by Chinstraps.

Intraspecific differences were found only in the diets of male and female Gentoo and

TABLE 4. Sexually mature (males + females) and adolescent euphausiids in pygoscelid stomachs.

Species	Euphausiids		
	Male (%)	Female (%)	Adolescent (%)
Adélie Penguin*	51.1	43.9	5.0
Chinstrap Penguin**	64.0	34.2	1.8
Gentoo Penguin	44.8	55.0	0.2

* χ^2 significantly different from Chinstrap ($P < 0.025$) and Gentoo ($P < 0.01$).
** χ^2 significantly different from Gentoo ($P < 0.005$).

Adélie penguins. Male Gentoos consumed significantly more fish (22.9%) than did females (7.3%; $\chi^2 = 5.985$; df = 1, $P < 0.025$). Male Adélie Penguins ate smaller euphausiids than did females ($P < 0.01$; ANOVA and Duncan's new multiple range test), although the difference was only 0.67 mm.

To assess seasonal variations in the characteristics of prey eaten, we analyzed stomach contents as a function of both the stage of the reproductive cycle (i.e., eggs only, eggs and chicks, chicks only; Table 5), and month when the samples were collected (Table 6). Male and female penguins ate similar prey over the course of the austral summer. The relative numbers of sexually mature and adolescent euphausiids eaten by the three penguins did not differ seasonally and all three species consumed significantly larger euphausiids as the reproductive cycle progressed (Tables 5 and 6). It should be noted, however, that only 3 of 34 Chinstrap Penguins examined in December had any food in their stomachs and the small sample obtained for that month was not analyzed. Significantly, interspecific differences among the three pygoscelids were consistent over months and stages of the reproductive cycle. The only exception to this was again the Chinstrap data for January–February, when these birds selected krill of about the same size class as those of Adélie Penguins.

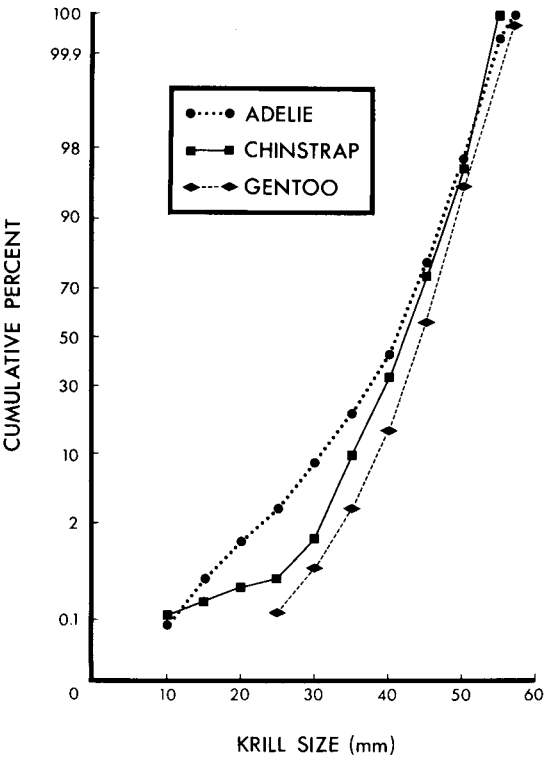

FIGURE 1. Cumulative percent of each size class of euphausiids consumed by the pygoscelid penguins.

DISCUSSION

Euphausia superba occurs in large dense swarms in the top 100 m of the water column. Its distribution is patchy, and the location and composition (size, class, age, sex) of these swarms is not yet well known. Consequently, it is difficult to determine whether pygoscelid penguins are preying on different populations of euphausiids. Several lines of evidence suggest, however, that pygoscelids forage in different areas and/or different distances from their breeding site: the differences in the duration of nest-relief among pygoscelids (Sladen 1958, Penney

TABLE 5. Mean lengths (±SE) of euphausiids consumed by the penguins over the course of their reproductive periods.

	Egg	Egg–Chick	Chick	ANOVA	*P*
Adélie	37.6*†	40.8*	41.7*	44.310	<0.005
n = 2,046	±0.5	±0.2	±0.2		
Chinstrap	41.3*†	42.2*	42.7*	8.477	<0.005
n = 1,190	±0.3	±0.3	±0.2		
Gentoo	44.3*	44.6*	45.3*†	8.522	<0.005
n = 2,014	±0.2	±0.2	±0.2		
ANOVA	158.000	105.000	69.712		
P	<0.005	<0.005	<0.005		

* Significantly different ($P < 0.01$—Duncan's new multiple range test) in vertical comparisons.
† Significantly different ($P < 0.01$—Duncan's new multiple range test) in horizontal comparisons.

TABLE 6. Mean length (±SE) of euphausiids consumed by penguins during the austral summer.

	November	December	Jan.–Feb.	ANOVA	*P*
Adélie Penguin	37.6*†	40.9*	41.8	98.500	<0.005
n = 2,046	±0.5	±0.2	±0.3		
Chinstrap Penguin	41.5*	NS	42.5		
n = 1,190	±0.4	—	±0.2	—	—
Gentoo Penguin	44.2*	44.1*	45.2*	84.780	<0.005
n = 2,014	±0.2	±0.2	±0.2		
ANOVA	44.690	32.571	10.610		
P	<0.005	<0.005	<0.005		

* Significantly different ($P < 0.01$—Duncan's new multiple range test) in vertical comparison.
† Significantly different ($P < 0.01$—Duncan's new multiple range test) in horizontal comparison.
NS = No sample (see text).

1968, Conroy et al. 1975b, this study); differences in the ratio of fresh to digested stomach contents; differences in the proportions of male, female, and adolescent euphausiids taken by each penguin species; and the large number of Chinstrap Penguins returning to the rookery with empty stomachs during the egg phase of their breeding season. Two recent studies support this hypothesis. Croxall and Prince (1980) reported that sympatrically breeding Gentoo and Macaroni penguins (*Eudyptes chrysolophus*) at Bird Island, South Georgia, preyed chiefly on large (40–65 mm) *E. superba*; they also presented evidence that these penguin species have different feeding ranges and areas. Ainley (pers. comm.) has seen pygoscelids frequenting different areas and habitats at sea. Another factor may be that these penguins feed at different depths. Gentoo Penguins are known to descend to depths of 100 m, while Adélie and Chinstrap penguins in the same region were reported to feed on krill at the surface (Conroy and Twelves 1972). The larger krill eaten by Gentoos (this study) argues for a deeper feeding depth, in that *E. superba* forms two layers during the day, the adults at deeper levels than adolescents (Marakov and Shetsov 1972, Everson 1977, Jazdzewski et al. 1978).

Ainley and Emison (1972) and White and Conroy (1975) also reported intra- and interspecific differences in the diets of pygoscelid penguins. Interestingly, the heterogeneity in diets was not the same. Ainley and Emison (1972) at Cape Crozier, Ross Island, in 1965–1966 reported that Adélie

TABLE 7. Reports of food habits of the pygoscelid penguins. Quantitative data included when available from literature.

Species	Locations	Diet (wet weight or volume)	Source
Adélie Penguin	Wilkes Land	Primarily krill	Levick (1915)
	Ross Sea	Primarily krill	Falla (1937)
	Palmer Land	Fish with some krill	Eklund (1945)
	Signy Island	Krill	Sladen (1958)
	Wilkes Station	Krill	Penney (1968)
	Ross Sea	60% krill; 39% fish; 2% amphipods	Emison (1968)
	South Orkneys	100% krill	White and Conroy (1975)
	South Shetlands	99+% krill	This study
Chinstrap Penguin	South Georgia	Krill	Murphy (1936)
	Graham Land	Primarily krill	Bagshawe (1938)
	Signy Island	Krill	Sladen (1955)
	South Orkneys	100% krill	White and Conroy (1975)
	South Shetlands	98% krill; 2% fish	Croxall and Furse (1980)
	South Shetlands	99+% krill	This study
Gentoo Penguin	South Georgia	Krill	Murphy (1936)
	Graham Land	Primarily krill	Bagshawe (1938)
	Heard Island	Fish, small number of krill & cephalopods	Ealey (1954)
	South Orkneys	Primarily fish, some krill	Conroy and Twelves (1972)
	South Orkneys	100% fish	White and Conroy (1975)
	South Georgia	67% krill, 33% fish	Croxall and Prince (1980)
	South Sheltands	85% krill, 15% fish	This study

TABLE 8. Comparison of body characteristics of pygoscelid penguins* at Point Thomas, King George Island.

Body characteristic	Relationship in decreasing size (mean in parentheses)**
Body weight (g)	G Males (5,500) > G Females (5,060) > A Males (4,500) = C Males (4,300) > A Females (4,200) = C Females (3,700)
Body length (mm)	G Males (652) = G Females (622) > A Males (580) = C Males (579) = A Females (563) = C Females (548)
Culmen length (mm)	G Males (50.8) = C Males (50.5) > G Females (48.4) = C Females (46.6) > A Males (41.5) = A Females (39.8)
Culmen width (mm)	A Males (20.2) = C Males (20.1) > C Females (18.5) = A Females (18.1) = G Males (18.0) = G Females (16.1)

* G Gentoo Penguin, A Adélie Penguin, C Chinstrap Penguin.
** Means compared with ANOVA and then with Duncan's new multiple range test (significance indicated at $P < 0.01$).

males ate larger *E. crystallorophias* than females, and they suggested that this difference was related to sexual size dimorphism. In light of our findings that females consumed the larger euphausiids, and the highly synchronous Adélie Penguin breeding cycle in which the male takes the first incubation shift of two weeks, we suggest that the heterogeneity of their diets is caused by short-term differences in food availability.

White and Conroy (1975) collected stomach samples from 10 Adélie, 10 Chinstrap, and 4 Gentoo penguins in 1972–1973 at the South Orkney Islands. They reported that Adélie Penguins consumed significantly larger *E. superba* than Chinstraps, and that Gentoos ate exclusively fish. Our data also indicated that both Adélie and Chinstrap penguins relied primarily on *E. superba*, however, the latter consumed the larger prey. We found, furthermore, that the Gentoo Penguin was dependent upon krill for 84.5% of its diet by wet weight. The differences between our results and theirs may have resulted from differences in sample size, sampling method, locality and/or time of the year in which samples were collected.

The food habits of the pygoscelid penguins are summarized in Table 7. Although the number of quantitative studies are limited, an overview of them suggests that the Adélie and Chinstrap penguins are heavily dependent on euphausiids. Reports on the diet of the Gentoo Penguin, however, vary from 100% fish to largely krill. Gentoo Penguins are heavier and larger than Adélie or Chinstrap penguins, and the maximum span between the tips of the opened beak (an indication of the size of prey that can be taken) is also larger than in their congeners (Zusi 1975; Table 8). Considered as a whole, these factors suggest that the Gentoo Penguin has a more catholic diet than the other two.

We suggest that this is because the Gentoo's larger size allows it more flexibility in the type of prey items it selects.

Our results, and those of the studies cited, suggest that differences in the geographical and temporal availability of food to pygoscelid penguins are partially responsible for differences in their diets. Whether these differences indicate that these penguins share their food resources (e.g., have spatially and temporally segregated foraging patterns) or that they forage on the most available food items, within the limits of their habitat preferences and feeding methods, is not yet clear. Long-term quantitative analyses of the birds' feeding preferences in single and mixed species rookeries, as well as sampling and behavioral observations on penguins feeding at sea, are now necessary.

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