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Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea

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Abstract We investigated the diet and aspects of foraging effort among Adélie penguins (*Pygoscelis adeliae*) breeding at three colonies on Ross Island, in the southwestern Ross Sea – Capes Royds, Bird and Crozier – during the chick-provisioning period of three austral summers, 1994–1995, 1995–1996 and 1996–1997. During the study period, pack-ice cover differed in waters off-shore of these colonies, by colony, seasons and year. Diet differed among colonies only slightly. The fish *Pleuragramma antarcticum* was the most important prey, especially during years or periods within years when little pack ice was present. With respect to krill, which composed the remainder of diet, juvenile *Euphausia crystallorophias* were consumed predominantly in a year of heavy pack-ice cover; more adult krill were consumed in 2 years when pack ice was sparse. Foraging trip duration differed by colony, season and year and was related directly to distance from the colony to the nearest pack ice. The amount of food brought to chicks increased as trip duration increased, to a point (2 days), but then decreased as duration increased further (up to 4 days). On the basis of data on mass of parents and of meal sizes to chicks, it appeared that on the longest trips more of the food gathered by parents was used for self maintenance; on the longest trips, parents lost body mass. Successful foraging during chick rearing, the period when adult foraging is most intense, appears to depend on the proximity of pack ice to nesting colonies for this penguin species.

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Introduction

It has long been known that Adélie penguins (*Pygoscelis adeliae*) are closely associated with pack ice in the Southern Ocean (e.g., Murphy 1936; Fraser et al. 1992). The reasons for the association are unclear, but recent studies indicate that pack-ice conditions (especially ice cover) can affect the reproductive success and viability of this species in contradictory ways (see also Smith et al. 1999). In the most southern portions of Antarctic seas, where extensive ice cover on the sea is a persistent feature, if the extent of cover is great, thus restricting access to food, then Adélie penguins experience reduced reproductive success (Ainley and LeResche 1973). However, in the northern portions of Antarctic seas, at the margin of the pack-ice zone, if ice cover is minimal or lacking altogether, then Adélie penguins again experience reduced reproductive success. Conversely, in these marginal pack-ice areas, more extensive cover leads to greater reproductive success and/or breeding population size (Trivelpiece et al. 1990; Fraser et al. 1992; Trathan et al. 1996; Smith et al. 1999).

With this apparent contradiction in mind, we studied the response of Adélie penguins to pack-ice cover by conducting research simultaneously at three geographically adjacent colonies, each of which experienced different ice conditions within the respective area where they foraged. Ross Island provides the southernmost of all Adélie penguin colonies, and the presence of pack ice in the vicinity is a continuous feature (see Zwally et al. 1983; Jacobs and Comiso 1989). We compared diet among penguins at the three colonies in 3 successive years, in one of which sea-ice cover was far less extensive than in the others. In the 3rd year of study, in conjunction with diet, we also determined foraging trip duration, food load size brought back to chicks, and foraging cost measured by change in adult body weight at each of the colonies.

The objective of our study, then, was to investigate variation in diet and foraging effort in Adélie penguins

as a function of pack-ice cover. We sought to explore the hypothesis discussed above, that pack ice-cover strongly affects the viability of Adélie penguin populations, by exploring the effects of how mesoscale spatial and temporal differences in ice cover might affect aspects of foraging behavior.

Materials and methods

Study area

We gathered data at three adjacent colonies of the Adélie penguin – at Capes Royds, Bird and Crozier – on Ross Island, southwestern Ross Sea, during the chick-provisioning period of three austral summers: 1994–1995, 1995–1996 and 1996–1997 (Fig. 1). These colonies are about 40–50 km apart. Data collection began on about 20 December (peak hatching of eggs) and ended about 28 January each year (onset of fledging). Our study areas included these three colonies and the adjacent ocean north to the latitude of Franklin-Island ($76^{\circ}30'$). On the other dimension, the study area extended from the fast-ice edge along the Victoria Land coast eastward in McMurdo Sound and the southern Ross Sea to 175°E . We used the fast-ice edge in a visual satellite image taken on 15 January 1997 to calculate and compare the amount of ocean area covered by sea ice in each year (see below).

Data collection

During the first two summers, we gathered diet samples at weekly intervals at Capes Bird and Crozier. Sampling was as close as possible in time at the two locations, but usually we could not be in both locations on the same day. During the third summer, we collected samples at all three colonies on the same day, because then we had persons stationed at each colony. We collected samples at weekly intervals, giving us 4–5 samples per colony per year. Diet sampling was by the water off-loading technique described by Wilson (1984). We did not attempt to obtain the entire load of each penguin by forcing water into the penguin 2–4 times (flushes), the usual procedure. Rather, we were satisfied with one large flush, and allowed the adult to feed the remainder of its food load to its chick(s) or digest the remainder itself. The average wet mass of our samples (after water was drained through a sieve) was 221.7 g (range 70–550 g), which we believe indicates a sample sufficiently large to be representative of what the penguin had in its stomach. Emison (1968) determined the average food load carried by a parent to be 400–600 g. We flushed 5–7 penguins, all of which had chicks, at each sampling session (i.e. each sample equaled data from 5–7 individuals). Adults chosen for sampling were not involved in any of the procedures outlined below.

During the third summer, 1996–1997, we employed a computerized scale to weigh parents as they entered and left one sub-colony at each study site (see Gendner et al. 1992; or Kerry et al. 1993, for details on a similar system). Each sub-colony was encircled by a plastic fence that forced the penguins to walk across the scale. This scale weighed each bird 12 times per second as it passed across, after tripping a photocell to turn on the apparatus. The scale tared itself automatically every 2 min to compensate for dirt, guano, snow, etc. After walking across the scale, each bird tripped a second photocell, thus allowing us to determine whether the bird was entering or leaving. The computer stored both the mass measurements and the photocell activity. We did not use data collected after 10 January, because chicks then began to cross the scale.

We had hoped that PIT (passively interrogated transponder) tags implanted in 70 individuals (35 pair) at each location would allow us to identify (ID) the birds being weighed (see Kerry et al.

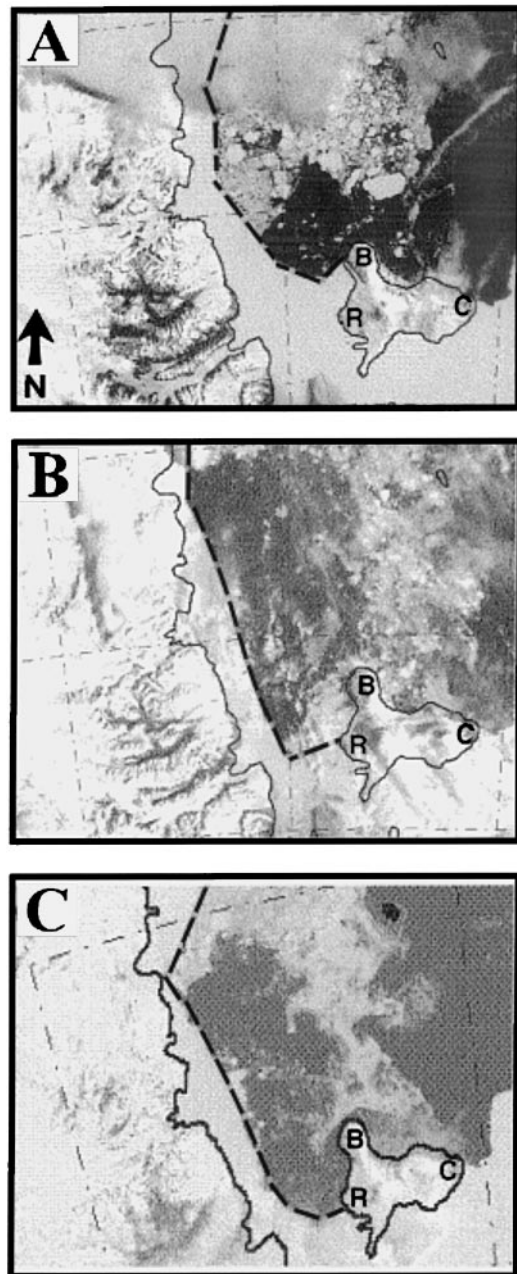


Fig. 1A–C Satellite images of the study area showing extent of pack ice on 1 January of each year of the study, 1995 (A), 1996 (B) and 1997 (C). In particular, note the position of the fast-ice edge (dashed line) in McMurdo Sound relative to location of the Capes Royds (R) and Bird (B) colonies

1993 for details). Among other things, doing this would allow us to determine the amount of time each adult was away foraging. This aspect of our apparatus, however, was still in the developmental stage and we were not able to gather suitable ID data for our purposes.

To gather data on foraging trip duration, we logged the presence/absence in the colony of penguins to which a small radio transmitter had been affixed to the lower back (20 g, <0.5% of body mass or body cross-section). Our sample comprised 15 breeding individuals at each colony. The black radios were attached using black plastic tape (see Wilson 1989; Wilson et al. 1990; Wilson et al. 1997). At each colony three times per day (ca. 0700, 1300 and 1800 hours) during the period 20 December to 10 Janu-

ary, we used a programmable receiver to determine whether or not each radio-affixed penguin was present. Thereafter, we removed the radios. All birds continued to feed chicks during the period of investigation.

Although we do not present the details herein, our radio telemetry in 1996–1997, when pack-ice cover was minimal (see below), indicated that Adélie penguins sought areas of pack ice in which to forage. Penguin positions were determined by triangulation (see Sadleir and Lay 1985 for discussion of technique, including location of some of the same listening posts). Penguins apparently did not forage in open water (judged by the characteristic of telemetry signals given by foraging penguins described in Trivelpiece et al. 1986). This pattern helped us to structure our analysis of ice conditions.

Pack-ice conditions were analyzed using satellite imagery obtained from Scripps Institution of Oceanography. We obtained every cloud-free visual image available within the period 20 December to 28 January for each year. We analyzed each one, but herein only results from widely spaced, representative images are shown. Images were prepared using Terascan software at McMurdo Station and Scripps Institution of Oceanography. Distances between colonies and pack-ice edge and areas of ocean covered by pack ice were calculated using the software package Gaia, an image-processing tool that can count pixels by color class, convert them to area and calculate distances (Shelley et al. 1993). We estimated the proportion of the study area covered by pack ice and distance between each colony and closest pack-ice edge for each image. We attempted to secure an image about every 5 days that was sufficiently clear of cloud cover to suit our purposes (Table 1). We used the fast-ice edge on 15 January 1997 (the minimum fast-ice coverage for the study) to define the ocean area influenced by sea ice (fast ice plus pack ice) in all 3 years.

Data analysis

The material from each stomach-flush sample was drained for ca. 20 s on a fine-wire mesh and then sorted by prey species. The

Table 1 Percent of study area covered by pack ice, and distance from each colony to closest pack ice, by date in each of 3 years. Distances in *italics* are across fast ice; others across open water

Date	Percent cover	Distance from colony to pack-ice edge (nm)		
		Royds	Bird	Crozier
1994–1995				
23 Dec 94		<i>30.5</i>	3.3	12.1
28 Dec 94	55	<i>21.0</i>	5.9	9.8
1 Jan 95	47	<i>22.6</i>	3.8	10.2
3 Jan 95	47	<i>24.1</i>	0.0	2.7
7 Jan 95	46	<i>13.5</i>	5.1	36.0
8 Jan 95	47	0.0	3.5	37.2
16 Jan 95	30	0.0	8.3	2.0
1995–1996				
30 Dec 95	30	0.0	0.0	1.5
7 Jan 96		0.5	4.1	6.6
10 Jan 96	35	1.7	0.5	22.0
14 Jan 96	57	0.0	0.0	17.7
19 Jan 96	54	0.0	0.0	
23 Jan 96	43	0.0	7.9	48.6
1996–1997				
24 Dec 96	37	0.0	2.4	25.0
28 Dec 96	25	0.0	0.0	29.0
1 Jan 97	10	0.0	6.8	21.3
3 Jan 97	15	0.0	0.0	29.0
14 Jan 97	10	5.6	6.7	72.1
22 Jan 97	0	10.5	16.8	37.3

contribution of each species by percent total wet mass was determined. Then, for each date and locality (a sample = five to seven birds), the percent contribution of each prey type was averaged. Fish species were determined by otolith shape and other characteristics (e.g., black peritoneal lining and hollow vertebrae in *Pleuragramma antarcticum*), and krill species by characteristics specified in Fischer and Hureau (1985).

We estimated the duration of foraging trips in days, with dates shown herein representing the departure from a colony. The frequency of our checks for the presence of radios (affixed to penguins) allowed estimation of trip duration to the nearest quarter day. We began the analysis on 23 December and ended on 10 January, although some birds returned 2–3 days later than 10 January (and were included). We ended on 10 January to allow about 7–10 days to recover radios (for use the next year); this brought us to about the onset of fledging, when chicks would disappear. In the statistical analysis of these data, when we related trip duration in days to distance-to-ice, we used the “lowess” procedure (locally weighting scatter plot smoothing; Cleveland 1979).

To estimate penguin mass for each crossing, we ignored the lower and upper 2.0-kg records, i.e. masses < 2.5 kg (a chick or an adult that hardly touched the scale on its rapid pass) and > 5.1 kg (likely more than one penguin; Fig. 2). This range of mass is in accord with the extensive weighing of adults and chicks undertaken previously on Ross Island by Ainley (1972) and Ainley and Schlatler (1972). All measurements (from the same crossing) that were within 0.1 kg of the maximum mass recorded for that crossing were averaged, provided that there were at least three such maximal measurements per crossing. The mass determined in this way included the bird’s stomach contents when a bird was passing into the subcolony. Statistical analyses were performed on the daily mean mass, in each direction, averaging values for all penguins in that day.

Statistical programs were taken from software provided by STATA (1993).

Results

Pack-ice conditions and foraging

Sea ice was extensive and persistent in 1994–1995 compared to the other 2 years; it was least extensive in 1996–1997 (Fig. 1). Accordingly, on 1 January 1995, the

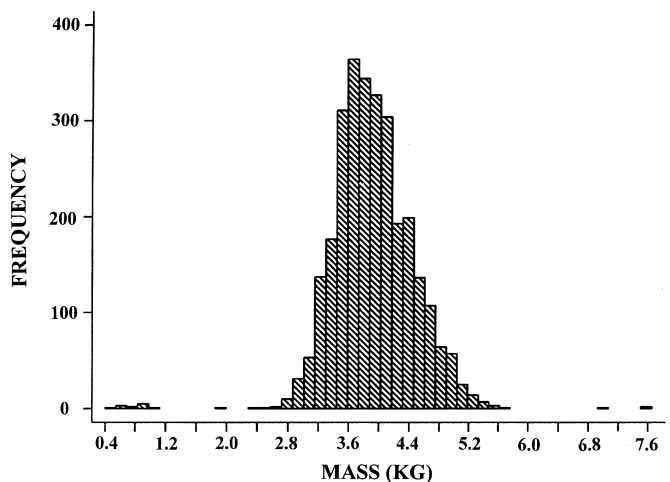


Fig. 2 A frequency histogram showing the masses recorded by the automatic scale, with 5.1 selected as the maximum mass allowed to represent one penguin

fast-ice edge was at Cape Bird, 24 nm (41 km) north of Cape Royds, compared to 1996 and 1997, when the edge was right at Cape Royds on that date. Thereafter in each summer, break up of the fast ice accelerated and its edge began to recede quickly. In the case of pack ice, satellite imagery indicated that cover in 1994–1995 was almost 50% of the study area through to 10 January (Table 1). In contrast, during both the latter 2 years, 1995–1996 and 1996–1997, cover at times was much less (15–35%).

In 1994–1995, parents from Cape Royds had to walk northward across 24 nm of fast ice to reach pack ice throughout the first third of the chick-provisioning period. At the same time, parents from Cape Crozier swam across ca. 35 nm of open water to reach pack ice, mostly to the west and northwest. In almost every year, the waters adjacent to Cape Crozier, especially to the east and north, are kept ice free during spring and summer by strong, persistent offshore winds (Zwally et al. 1985; Bromwich et al. 1992); Cape Crozier is usually at the edge of a large polynya (see Zwally et al. 1983; Jacobs and Comiso 1989). In the next 2 years, 1995–1996 and 1996–1997, fast-ice and pack-ice cover were much reduced. Crozier birds had to swim as much as 72 nm across open water to reach pack ice (Fig. 1B, C). Penguins from Cape Bird, which at first was close to the pack-ice edge, had to swim at most 17 nm to the ice. Parents from Royds had to swim even less, at most 10.5 nm, to reach the pack ice; fast ice was to the south.

Diet composition

During summer 1994–1995, four and five weekly diet samples (food from five to seven individuals in each sample) were obtained from Cape Crozier and Cape Bird, respectively. Fish, mainly *Pleuragramma antarcticum*, contributed 60–70% of the diet at Cape Crozier but only 10–20% at Cape Bird (Fig. 3A). Euphausiids, principally *E. crystallorophias*, especially at Cape Bird, contributed the remainder, except for 1–2% sometimes contributed by amphipods. In fact, at Cape Bird *E. crystallorophias* dominated the diet, with fish increasing slightly in prevalence as time passed. The euphausiids were about 21–23 mm in length, the size range of the subadults of this species (Fischer and Hureau 1985).

In summer 1995–1996, the diet was markedly different (Fig. 3B). As in 1994–1995, the importance of fish increased as time passed, but subadult *E. crystallorophias* were rarely eaten. Instead, the main euphausiid eaten was adult *E. crystallorophias*, in a size range of 28–34 mm length (thus, adult in age). Overall, fish (*Pleuragramma antarcticum*) and *E. crystallorophias* contributed about 50% each, with the fish increasing and the krill decreasing as time passed.

In summer 1996–1997, the diet of birds breeding at Cape Bird was very similar to the pattern evident the previous year (Fig. 3C). In contrast, fish were much more prevalent in the diet of Crozier birds than in pre-

vious years, but again increased within the year as time passed. *E. crystallorophias* (again, subadult) was much less important. During this year, we also had samples from Cape Royds; there, fish dominated throughout, except for the very last date, when krill resumed in importance.

Foraging trip duration

Foraging trips at Cape Crozier during the first 2 weeks of chick rearing in 1996–1997 lasted about 2 days (Fig. 4A). Then, beginning on 5 January the average reached 3.5 days, followed by a reduction in length thereafter (9 January). At Cape Bird (Fig. 4B), trips generally were 1 day long, but after 1 January they lengthened to almost 2 days, followed by a return to 1-day trips after 7 January. Finally, at Cape Royds trips lasted on average slightly longer than 1 day throughout the study period (Fig. 4C).

Trip duration was related to distance to the nearest pack ice ($\beta_2 = 0.2034 \pm 0.053$, $P = 0.002$, $N = 17$ days). At Cape Crozier during the period 24 December 1996 to 3 January 1997, trip duration increased slightly even though distance-to-ice was unchanged. Thereafter, however, distance-to-ice increased markedly as did, in concert, trip duration.

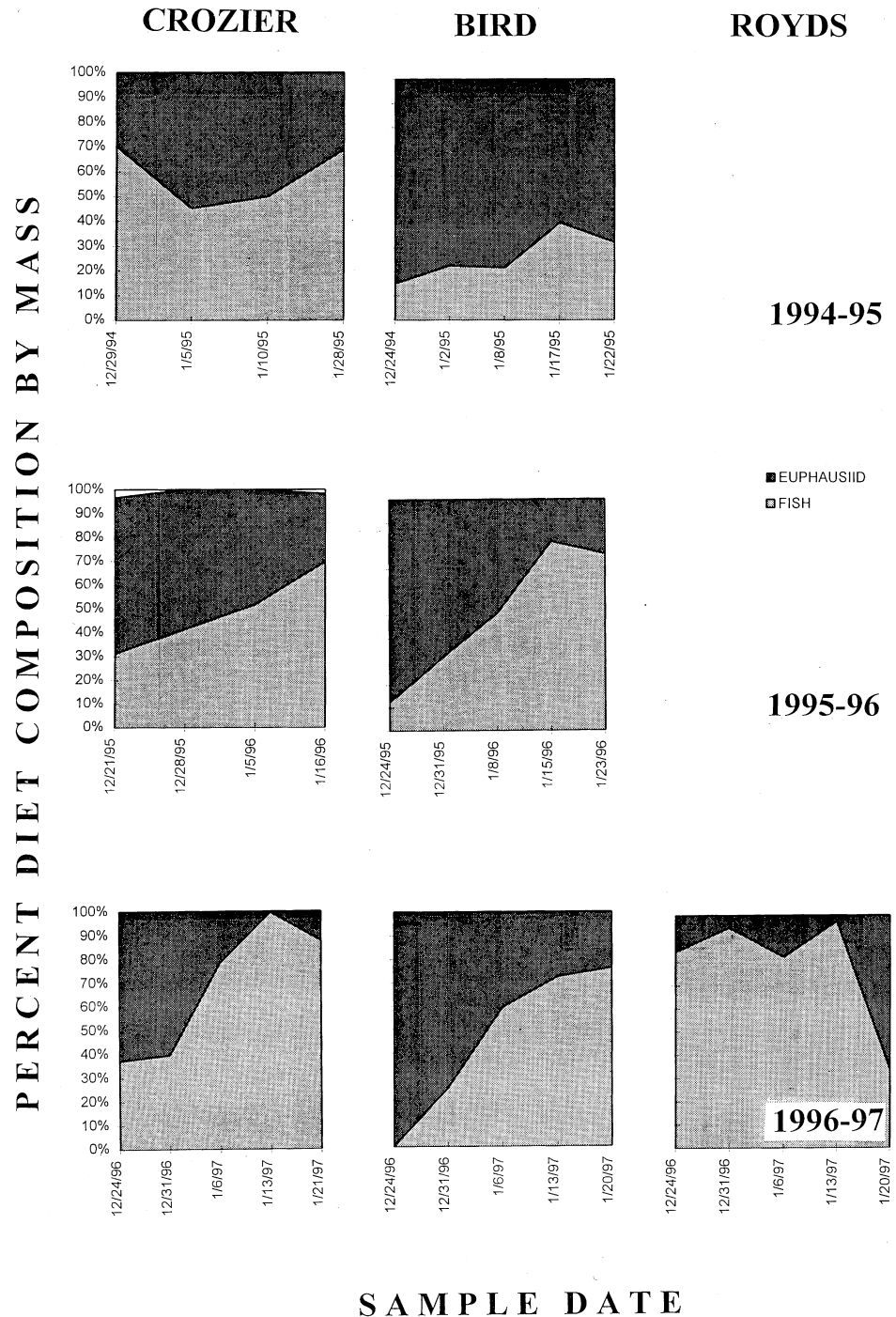
Mass of food delivered to chicks

Over the entire chick-provisioning period in 1996–1997, the mass of parents at Capes Royds and Bird averaged 4.11–4.13 kg upon arrival to feed their chicks and averaged 3.83–3.84 kg after off-loading their prey (Table 2). In contrast, arriving Crozier parents weighed only 3.83 kg before feeding chicks and 3.66 afterward. This means that the meals fed by each parent to chicks at Royds and Bird (270–300 g) were 57% heavier than the meals fed at Crozier (130 g).

In actuality, meal mass at all three locations began at about the same level (ca. 200 g; Fig. 5). As time passed, however, meal mass at Bird and especially Royds increased, while that at Cape Crozier decreased. This difference in meal mass between colonies is statistically significant (Table 3).

Another way to look at this pattern is to relate meal mass fed to chicks to the amount of time that parents were away obtaining the food. At Capes Bird and Royds, Adélie penguins behaved according to optimal foraging theory (e.g., Stephens and Krebs 1986) and brought back heavier loads when they stayed away or trip distance was longer (Fig. 6; recall that trip distance related to trip duration). Trip duration, however, rarely exceeded 24 h, as already noted. At Cape Crozier, where trips usually exceeded 24 h, parents brought back less food on the longest trips than they did on the shortest ones. Therefore, they were not foraging optimally, at least according to theory. The difference in trend be-

Fig. 3 Percent composition by mass of the Adélie penguin diet, by date and sample locality, during three austral summers, 1994–1995, 1995–1996 and 1996–1997; each date represents the average percent for the five to seven samples collected at the respective localities



tween colonies (increasing prey load with increasing trip length at Capes Bird and Royds; opposite trend at Cape Crozier) is statistically significant: $P = 0.002$ for difference between Crozier and either Bird or Royds; $P > 0.8$ for difference in trend between Bird and Royds. A further indication that foraging became less than optimal for Cape Crozier parents, on a practical (as opposed to theoretical) basis, was the fact that they actually lost body mass much more quickly than parents at the other sites as the season progressed (Fig. 7).

Discussion

Diet composition and ice cover

When we began this study, on the basis of studies by Emison (1968) and Van Heezik (1988), we expected that the diet composition of Adélie penguins, if it varied either annually, seasonally or among colonies in the southern Ross Sea, would do so in the amount of krill (essentially *Euphausia crystallophias*) relative to fish (mostly *Pleu-*

Fig. 4 Mean duration of foraging trips (days) taken by Adélie penguins from the Capes Crozier, Bird and Royds colonies by date in the austral summer, 1996–1997. Numbers along the top of each cell denote sample size (number of trips)

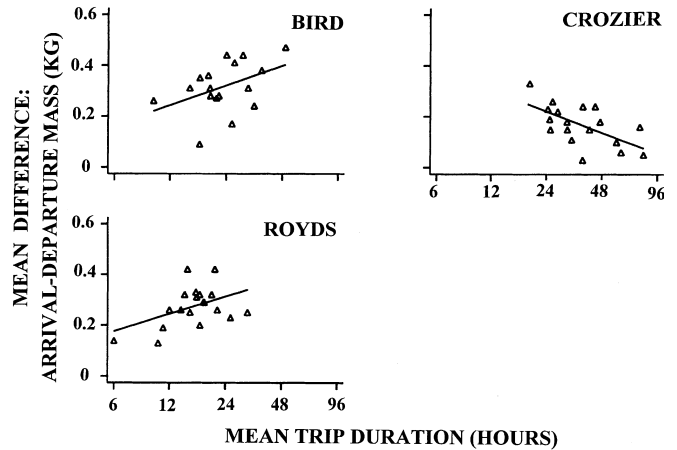
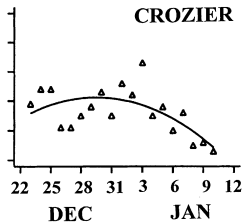
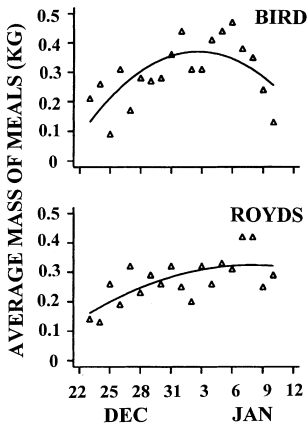
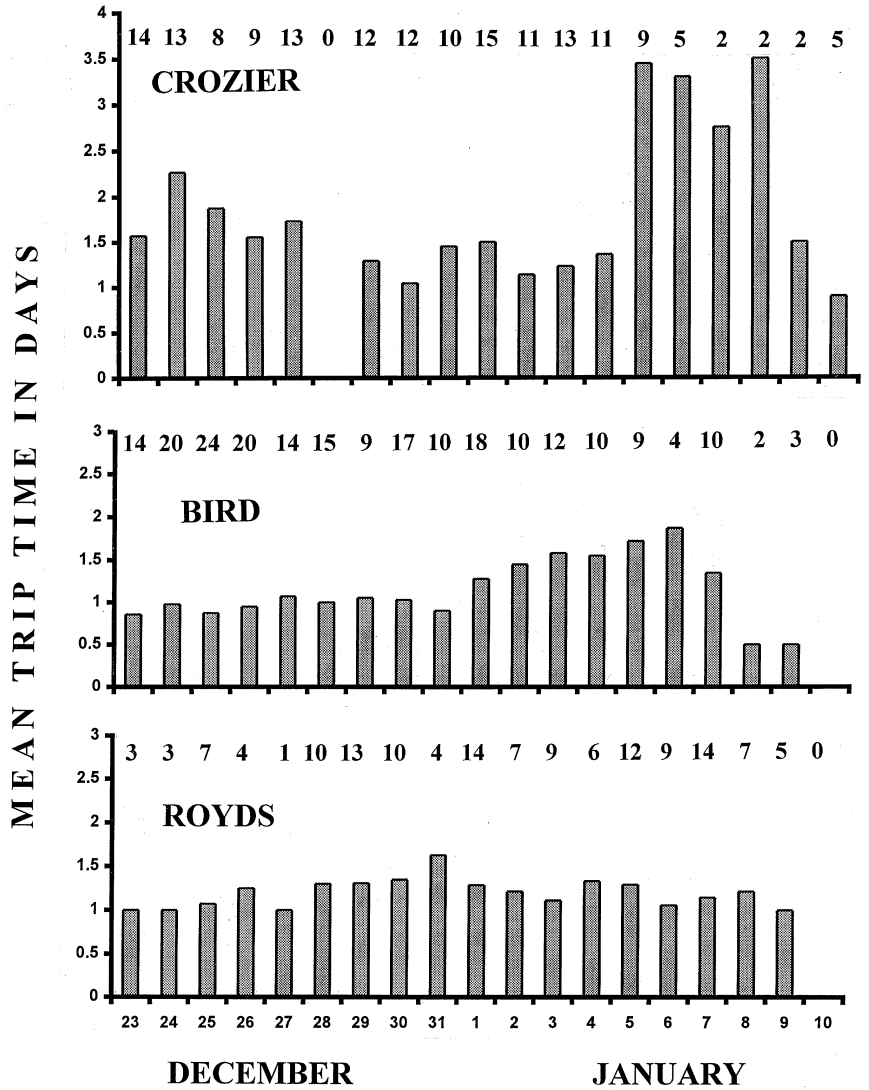


Fig. 5 Average mass of meals fed to chicks at the Crozier, Bird and Royds colonies by date during the austral summer, 1996–1997. Meal mass was determined by subtracting the mass of adults after feeding chicks from their mass before doing so; date on the x-axis is expressed as the number of days after 30 November (see Table 3 for statistical details)

Fig. 6 Difference between the mass of birds arriving and those departing relative to (log) duration (h) of the foraging trip, austral summer 1996–1997: Cape Bird, not significant ($P = 0.081$); Cape Crozier, significant ($P < 0.01$, $R^2 = -0.620$); Cape Royds, significant ($P = 0.049$, $R^2 = 0.457$)

Table 2 A comparison of average body mass (kg \pm SE) upon arrival and departure of parent Adélie penguins at the Roysds, Bird and Crozier subcolonies, chick-provisioning period 1996–1997 ($N = 19$ daily means)

Colony	Mass IN	Mass OUT	Difference
Crozier	3.83 \pm 0.04 ^a	3.66 \pm 0.04 ^b	0.16 \pm 0.02 ^a
Bird	4.13 \pm 0.03	3.83 \pm 0.04	0.30 \pm 0.02
Royds	4.11 \pm 0.02	3.84 \pm 0.03	0.27 \pm 0.02

^aSignificantly different from both Bird and Roysds, $P < 0.0001$

^bSignificantly different from Bird ($P < 0.001$) and Roysds ($P = 0.002$)

Table 3 Linear trends in daily average body mass by date of adult Adélie penguins at the Roysds, Bird and Crozier colonies, chick-provisioning period 1996–1997 ($N = 22$ dates)

Colony	Slope ($\beta_1 \pm$ SE)	R^2	P
IN mass:			
Crozier ^a	-0.0205 \pm 0.0043	0.571	< 0.001
Bird	-0.0158 \pm 0.0031	0.598	< 0.001
Royds	-0.0118 \pm 0.0026	0.537	< 0.001
OUT mass:			
Crozier ^{b,c}	-0.0141 \pm 0.0058	0.259	0.026
Bird ^c	-0.0227 \pm 0.0038	0.672	< 0.001
Royds ^c	-0.0206 \pm 0.0024	0.819	< 0.001
IN-OUT difference:			
Crozier ^d	-0.0642 \pm 0.0030	0.215	0.046
Bird ^e	0.0069 \pm 0.0042	0.137	0.12
Royds	0.0089 \pm 0.0026	0.414	0.003

^aQuadratic trend also significant: $\beta_2 = 0.0025 \pm 0.00066$, $P = 0.047$; linear trend at Crozier different from Roysds (*a priori*, $P = 0.001$)

^bQuadratic trend significant: $\beta_2 = 0.00378 \pm 0.00077$, $P < 0.001$; linear trend significant from Roysds ($P = 0.027$) and Bird ($P = 0.017$)

^cLinear trends not significantly different

^dQuadratic trend also significant: $\beta_2 = -0.00126 \pm 0.00054$, $P = 0.034$; linear trend significant from Roysds ($P = 0.0004$) and Bird ($P = 0.014$)

^eQuadratic trend significant: $\beta_2 = -0.00211 \pm 0.00071$, $P = 0.009$; linear trend not significant from Roysds

ragramma antarcticum). Generally, it is accepted that these krill and fish species characterize the fauna of persistently ice-covered waters that overlay the southern continental shelves in Antarctica, especially in the Ross and Weddell Seas (Marr 1962; Fischer and Hureau 1985, Hopkins 1987, Eastman 1993). These prey dominated the diets of Adélie penguins in the Emison and Van Heezik studies and did so, as well, in the diets of other predators of ice-covered neritic waters in the region, e.g. Weddell seals (*Leptonychotes weddelli*) (Plötz et al. 1991) and emperor penguins (*Aptenodytes forsteri*) (Cherel and Kooyman 1998).

Therefore, it was no surprise that the diet of Adélie penguins in our study was dominated by *E. crystallophias* and *Pleuragramma antarcticum*. What was surprising, however, was the predominance of fish. Fish was a minor component of the diet in both Emison's (1968) and Van Heezik's (1988) study. At this point, it is difficult to say whether or not we have detected a change in the availability of potential prey for Adélie penguins in the southern Ross Sea. We collected data for three

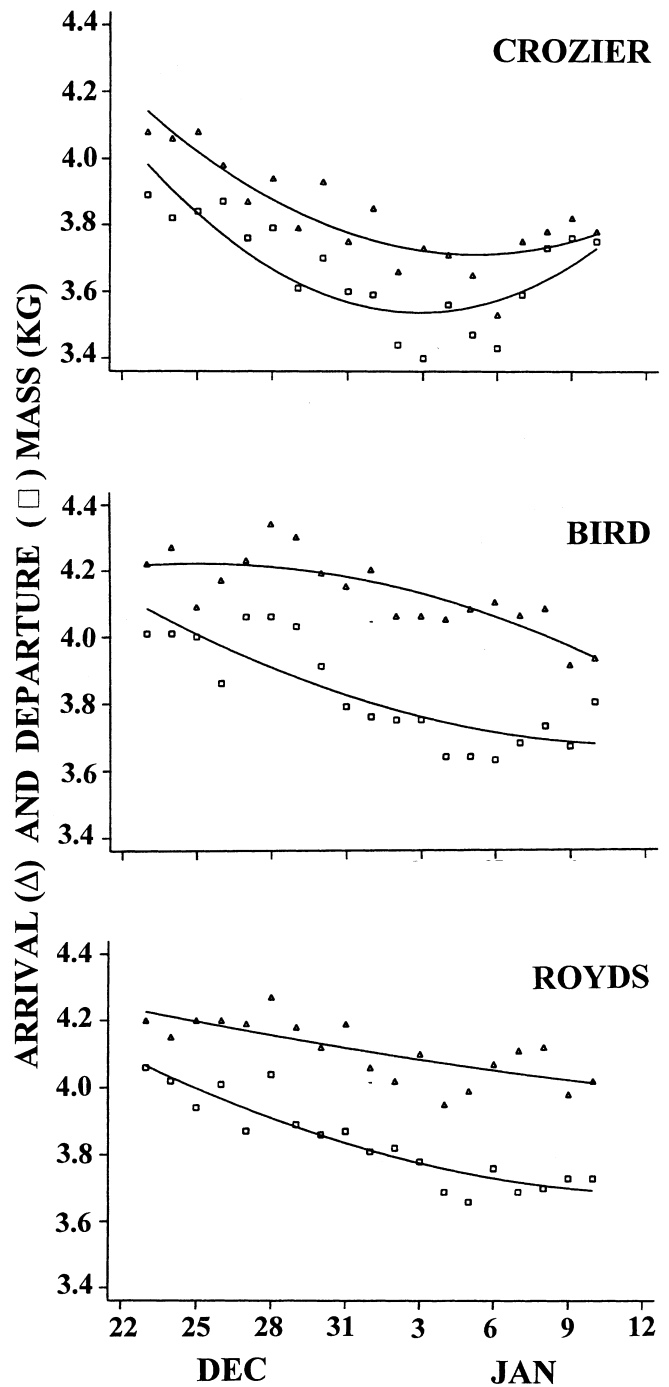


Fig. 7 A comparison of body mass of parents before and after feeding chicks at the Crozier, Bird and Roysds colonies in 1996–1997; statistical analyses are presented in Table 3

summers in the late 1990s; Emison collected data for two summers in the early 1960s, and Van Heezik collected data for one spring in the mid-1980s. What may be indicated here is that a short-term study cannot be used to characterize, overall, the relative prey composition of Adélie penguin diet, fish versus krill.

At the least, then, the data show that penguin diet can vary noticeably over short distances and short time spans. Subadult *E. crystallophias*, and krill in general, were

more prevalent in the diet in a year of heavier ice cover. These results agree with research on the relationship of ice cover to age composition of another krill species that has been studied much more exhaustively, *E. superba* (Kawaguchi and Satake 1994; Loeb et al. 1997). Fish appeared to be more prevalent in the diet in years of lower ice cover. Why penguins from Cape Bird ate slightly more krill than those at Capes Royds and Crozier is an enigma, because Cape Bird is mid-way between the other two colonies. Cape Bird, generally, was closest to pack ice. Therefore if, spatially, more ice means greater availability of krill and less availability of fish, the result is consistent with temporal variation in diet, i.e. more krill during the year when ice cover was most extensive and more krill earlier in the summer when ice cover again is more extensive. We will be exploring this spatial and temporal variation in diet more thoroughly in the future.

Foraging effort and ice cover

That heavy ice cover impedes (or increases) the reproductive and foraging effort of Adélie Penguins, as described by Ainley and LeResche (1973), is understandable in terms of the increased effort and time required to walk over treacherous, broken and re-frozen sea ice compared to swimming through open seas. In such a case, extensive ice cover leads to foraging trips so long that the food gathered is used by the adult rather than being devoted to chicks. In the case of much less extensive ice cover which, as described by Trivelpiece et al. (1990), can also affect reproductive effort of Adélie penguins (i.e., higher success with more ice), the mechanism involved has not been so apparent. Our results, however, help to understand the mechanism better.

Assuming that Adélie penguins seek areas of pack ice or pack-ice-influenced waters within which to forage, as our (unpublished) telemetry results indicated, when there is no ice, as described by Trivelpiece et al. (1990; see also Fraser et al. 1992), they do poorly in their reproductive activities. In our study, when the only pack ice in the region was a long distance from Cape Crozier, foraging trips grew much longer in duration (and, presumably, distance) than at other colonies (where the distance-to-ice was shorter) and adults brought back (or at least fed their chicks) significantly less food (see below). The indication is that on these long-lasting trips (almost 4 days vs 2 days long), the adults digested part of the food load on the way back to the colony and meals to chicks were smaller. Therefore, more of the parental foraging effort was devoted to self maintenance (see also Monaghan et al. 1989). It appeared, even, that the penguins that had to forage a great distance from the colony were no longer foraging optimally (longest trips resulted in the smallest meals to chicks). This was never the case for penguins at Capes Royds or Bird.

In the end, Crozier adults lost mass more quickly and chicks grew much more slowly and reached lower body

mass (3.2 vs 2.9 kg, respectively; unpublished data) than they did at Royds. The diet at both localities was the same, which means that a difference in food quality could not explain the differences. Additional research is needed to determine why pack ice is so important as a foraging habitat for Adélie penguins. As indicated by Watanuki et al. (1993), who investigated foraging near fast ice, fast ice apparently does not duplicate the qualities of pack ice, perhaps because the penguins can quickly deplete the available prey under that portion of fast ice accessible from near to the fast-ice edge.

Parental food loads and chick meal size

At the beginning of the chick-provisioning period, adults from each of the three study colonies delivered meals of the same mass, i.e. 200–300 g each, as determined by comparing adult mass before and after feeding the chick(s). It is well known that once the chick period begins, and adults begin to feed chicks, food loads (i.e. the amount of food in the adult's stomach) quickly increase in mass and, thereafter, remain at the asymptote regardless of the chick age or size (Emison 1968; Lishman 1985; Trivelpiece et al. 1990). What we find of interest here is that researchers who have measured the amount of food delivered to chicks by forcing adults to regurgitate (and then weighing the sample) have found food loads to be of the order of 300–600 g (e.g. Emison 1968; Trivelpiece et al. 1990; Watanuki et al. 1997), compared to the 200–300 g determined by our method. Therefore, our method determines meal size and not food load. Our results agree with those of Lishman (1985), who determined meal size by weighing chicks, rather than adults, before and after feeding. It appears that chicks receive about one-third to one-half of the amount of food captured by parents, but the ratio should be confirmed by additional, directed research.

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