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Moult habitat, pre- and post-moult diet and post-moult travel of Ross Sea emperor penguins

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ABSTRACT: During a series of transect legs through the pack ice of the eastern Ross Sea, aboard the RV icebreaker 'Nathaniel B. Palmer', we: (1) assessed the habitat chosen for moulting by emperor penguins, *Aptenodytes forsteri*, (2) determined their pre- and post-moult diets, (3) measured the pre- and post-moult body mass of the birds, and (4) tracked their post-moult movements. Diet was based on the colour of guano near the edges of ice floes and fast-ice areas. Pre- and post-moult birds were weighed at locations along the transect. Satellite transmitters were attached to 7 birds, and tracked for up to 5 mo. Birds moulted in concentrated pack ice and coastal fast ice. Offshore from the shelf slope, diet was mostly Antarctic krill *Euphausia superba*. Over the shelf, the diet was mainly fish and squid. Body masses of birds immediately after the moult were often less than 20 kg. After moult, satellite tracked birds remained in the pack ice but moved to the west at a rate of 13 to 41 km d^{-1}. One bird traveled to the Cape Roget colony, where it arrived on 15 April after 70 d and 2140 km of travel. We conclude that (1) birds are close to starvation by the end of the moult, (2) it is essential that an abundant food supply is in close proximity to the moult area, (3) penguins travel more than 2000 km on the return journey to their colonies of the western Ross Sea, and (4) reduction in the extent and seasonal duration of the pack ice would be reflected in a rapid change in the size of the breeding population of coastal west Antarctica.

KEY WORDS: Satellite transmitter · Eastern Ross Sea · Antarctica · Pack ice · Krill · Body mass · Emperor penguin

INTRODUCTION

Emperor penguins lay their eggs, incubate, and breed on fast ice near the continent of Antarctica during the austral winter (Wilson 1907, Stonehouse 1953, Prévost 1961). Studies in the 1960s and 1970s documented aspects of colony life, natal philopatry, breeding age, fasting physiology, and the discovery of more colonies (Budd 1961, Cranfield 1966, Stonehouse 1966, 1968, Stirling & Greenwood 1970, Isenmann 1971, Jouventin 1975, Le Maho et al. 1976). This was followed by research in the 1980s and 1990s on habitat, foraging areas, diets, diving behaviour using retrievable instruments, and foraging tactics observed from semi-captive birds diving from isolated holes in fast ice (Kooyman 1993, Kooyman & Kooyman 1995, Kirkwood & Robertson 1997a,b, Ponganis et al. 2000). However, until recently, aspects of their distribution, movements, and biology from the time they leave the breeding colony to moult to when they return to lay eggs, were unknown.

Kooyman et al. (2000) tracked 12 pre-moult emperor penguins that departed from 4 different breeding colonies near the Victoria Land coast. Normally the adults leave the colonies from mid-December to mid-January. After leaving the colonies, the birds traveled an average direct distance of 1200 km to the large consolidated pack ice area in the eastern Ross Sea,

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where they moulted. Following completion of their moult it was uncertain when the birds left the eastern Ross Sea, and when they returned to the colonies to breed again. Arrival at the colonies would most likely occur sometime in late March through April. Thus, during our cruise into this area (Ackley et al. 2003), we were interested in observing the type of habitat used by the birds when they were away from the coastal breeding colonies. We hypothesized that this was the most energetically demanding period in their annual cycle. Our reasons were as follows: (1) they must travel a direct distance of 1200 km to reach a reliable ice field on which to moult; (2) in addition to meeting the energy requirements for this trip, they must increase their body mass from an average of 25 kg at the time of departure from the colony (Kooyman et al. 2000) to nearly 40 kg in order to withstand the weight loss that will occur during the moult; (3) this gain in weight requires a reliable and abundant prey source during travel or at the site of the moulting area; (4) the moult area and its associated ice characteristics must be large and stable enough to sustain the 100000 birds coming from the western Ross Sea for a period of at least 2 to 3 mo; (5) during this period the birds must select individual floes that will remain intact for approximately the 30 d that the birds must remain out of the water while their plumage undergoes a complete replacement — floe selection has to be successful in the face of warming conditions and the declining pack ice; and (6) there must be an abundant and accessible food source in the epipelagic zone at or near the moult site. If this combination of special needs cannot be met, then prospects for the survival of the adult birds are poor. The least negative result would be a failure to breed during the next reproductive season. At worst, birds might die of starvation. Either result will be reflected in a decline in the breeding population and/or fledging success at the source colonies in the western Ross Sea within the same year. In contrast, an unusual abundance of food in the moult region combined with satisfactory pack ice would result in birds being able to breed during the following winter.

In this paper, we report on observations made of the pack ice conditions chosen by emperor penguins moulting in the eastern Ross Sea, their pre- and post-moult body mass and physical condition, qualitative aspects of their diet, and their travel rate and distance after the moult.

MATERIALS AND METHODS

We occupied the ice observation tower of the RV icebreaker 'Nathaniel B. Palmer' (NBP) from 28 December 1999, when we entered the pack ice at 69° S, until 7 February 2000, when we arrived at Cape Colbeck. Observations were continuous at all times after the ship had begun its journey. During that time, we made a west to east transit of the coastal polynya along Marie Byrd Land, and 4 north-south transits through the pack ice of the eastern Ross Sea. Each northbound transit reached the northern edge of the pack ice (Fig. 1). From the 26 m-high observation tower of the NBP, we

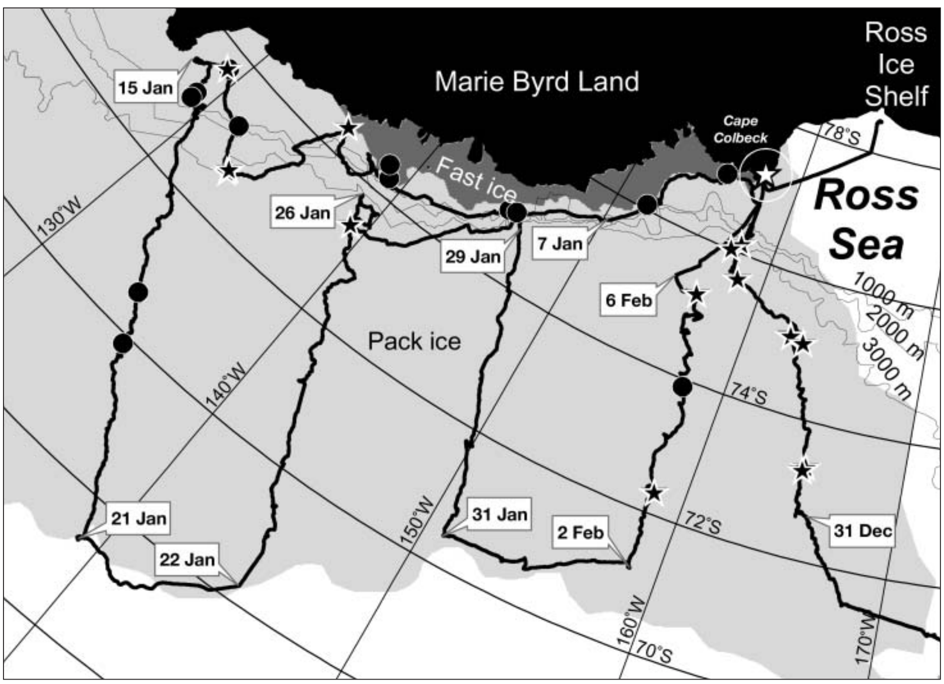


Fig. 1. Study area and cruise track (thick line) of the Antarctic Pack Ice Seals (APIS) Programme from December 1999 to February 2000 in the eastern Ross Sea. Coverage of pack ice (light shading) and fast ice (dark shading along coast) during the cruise are from data provided by the US National Ice Center. The ship's progression is shown by date. Penguin scats observed along the ship's track: ● are mainly fish vertebrae, otoliths, and squid beaks; ★ are mainly krill parts (see Table 1); ☆ one of the largest emperor penguin colonies in the Ross Sea

recorded our observations on a standardized form, which included sea-ice conditions, emperor penguin numbers and distribution, and the colour of the penguin scats (which we hypothesized would indicate their general diet composition). Only when emperor penguins were associated with the scats did we record the colour that we saw.

Scat analysis. With few exceptions, emperor penguin guano was either black or red, both of which were visible from the ship when it was within 100 m of the ice edge. While working on the sea ice, we also collected scat samples in plastic bags to determine the relationship of scat content to colour. Samples of similar colour were pooled. Soon after collection, the samples were analyzed aboard the ship. Verification of dietary contents of the 2 dominant scat colours, black and red, was made by separating the contents and identifying them with modification of the standard scat analysis suggested for birds (Croxall 1993). Scats were washed and filtered through 3 meshes of screen sized 500, 1000 and 2000 mm. The contents of the screens were flushed into 30 cm-diameter black sluicing pans, and krill carapaces, eye stalks, squid beaks and otoliths were sorted. The beaks and otoliths were stored dry in small bottles or under slides with coverslips for later species identification.

Determination of mass. During the cruise, we left the ship numerous times to capture and weigh penguins, and sometimes to attach satellite transmitters. Captured birds were physically restrained briefly while a hood was put on the head and a harness quickly attached. Once under control, birds were suspended from a 50 kg Pesola scale, with 500 g divisions, that was hooked to the harness.

Satellite tracking of individual birds. Between 28 January and 6 February 2000, we attached Sirtrack, Kiwi model 101, satellite transmitters or platform transmitter terminals (PTT) to 7 post-moult birds. PTTs were attached to the bird's feathers with Loctite 401, a fast-drying cyanoacrylic glue, and stainless steel cable ties. The PTTs were imbedded in smooth, black plastic and streamlined to reduce drag. They had an average mass of 195 g (<1% of body mass), and measured 14 cm long by 5.5 cm at the widest part of the taper to the posterior, and 1.6 cm at the maximum thickness in the aft part of the tapered profile. The antenna exited at an angle of 20° from the horizontal axis of the transmitter body. Transmitters were mounted well forward on the bird (just posterior of the maximum girth) to ensure that when the bird was in the water, the antenna was in the air and could transmit effectively.

Six transmitters used a salt-water detector programmed to function as a salt-water switch (SWS). In 5 of the transmitters the SWS stopped transmissions any time the unit was submerged (bird diving), or when the bird got out of the water for more than 3 h. When the bird re-entered the water, the transmitter would restart once salt water was detected. The 6th transmitter incorporated a SWS to detect when the bird was diving. During the dive, transmissions ceased, but resumed again when the bird surfaced. This transmitter ran for 12 h and was off for 12 h. A 7th transmitter (bird 18902) had no SWS and simply was on for 12 h and off for 12 h, and continued to cycle for the entire life of the batteries.

Specific locations were determined from Argos Class 1 to 3 quality locations only. The least accurate of the 3 classes is a geographical fix at <1 km radius. Only 1 location d^{-1} was used for construction of the tracks and estimation of daily travel rates. Times as close to midday as possible were chosen for the estimate.

Ice data. The pack ice distribution and concentration data were obtained from weekly US National Ice Center (NIC) reports, which use a variety of microwave and visible data sources from polar orbiting satellites.

RESULTS

Ice conditions and emperor penguin distribution

From January through February, when the birds were seeking a moult site, the sea ice coverage was shrinking rapidly, with a nearly complete decay in the western Ross Sea (Fig. 2). However, the summer ice

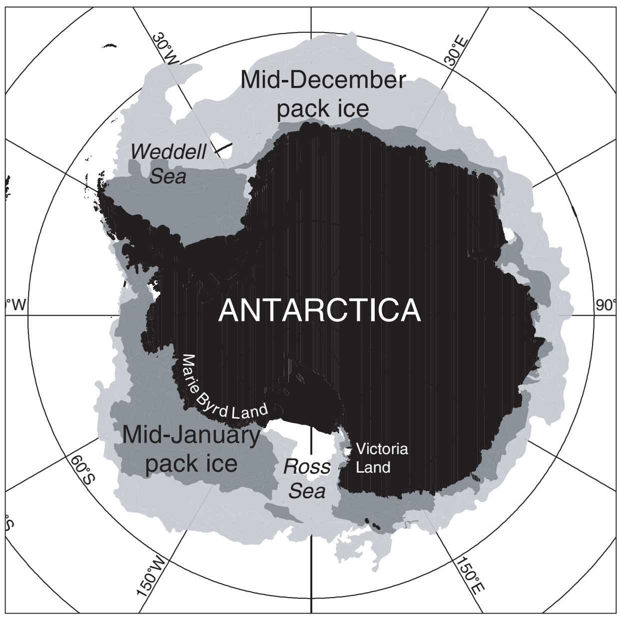


Fig. 2. Antarctic circumpolar sea ice distribution in mid-December 1999 and mid-January 2000. Note the exceptionally large amount of January pack ice in the eastern Ross Sea at the time of the survey, compared to the rest of Antarctica. Sea ice data were provided by the US National Ice Center

Fig. 3. Large ice floe in the eastern Ross Sea, showing the surface relief that provides protection from the wind to birds moulting in the interior of the floe (photo by G. Kooyman)

field in the eastern Ross Sea is consistently the largest in Antarctica, and it is also a region of exceptionally large floes. One of the largest floes we witnessed, ca. 20 by 40 km, had several groups of moulting penguins dispersed across its surface. Pressure ridges of ice on both large and small floes sheltered the penguins from wind, and consequently reduced convective heat loss (Fig. 3).

In areas to which birds had been previously tracked (Kooyman et al. 2000) we found emperor penguins in abundance. Approximately 11000 birds were counted during our tower watches, a number exceeded only by that of crabeater seals *Lobodon carcinophaga.* Six other species of marine birds and mammals were noted (*Pygoscelis adeliae*, *Leptonychotes weddellii*, *Hydrurga leptonyx*, *Ommatophoca rossii*, *Orcinus orca*, *Balaenoptera acuterostrata*). The majority of emperor penguins were on large floes or coastal fast ice. There was a mix of adult and juvenile birds in all stages of moult, from those that had not begun to those just finishing. On the large floes, birds deep into moult were located in the interior, while numerous birds that had either finished moult or had not started the 30 d moult and fast predominated along the edges. These ice-edge birds were going in and out of the water. We estimate emperor penguins probably use this area for moulting from late December to mid-March.

Scat analysis

We collected 51 scat samples from 11 locations (Table 1). The dietary contents of black versus red scats were consistent and clear. Red guano consisted almost entirely of krill carapaces, which were absent in the black scats, and which in turn contained mainly squid beaks and otoliths (Table 1). Based on the association of the guano colour with prey type, we concluded that recording of scat colour from the tower would be a good assessment of the pre- and post-moult diet of emperor penguins in this area. Most otoliths were from the Antarctic silverfish *Pleuragramma antarcticum*. Otoliths from samples offshore from the shelf were not identified. Since the prey had been digested before discharge as guano, these analyses were qualitative as we were unable to measure the proportional differences in prey taken.

The geographic distribution of red and black scats was consistent, with a few outliers (Fig. 1). Scats that were coloured green or yellow were few in number and contained no food items. Therefore, they were not included in Fig. 1. The brown-coloured guano probably represents a mix of fish and krill, and also seemed to be few in number. Eight of the locations reported for black scats were near the continent over the shelf,

Table 1. *Aptenodytes forsteri*. Summary of scat collections and analysis for evidence of the prey type, based on colour of the guano (January to February 2000). Chitin: zooplankton exoskeleton, *P.a.* = *Pleuragramma antarcticum*; *P.g.* = *Psychroteuthis glacialis.* Identification based on Fischer & Hureau (1985)

No. and colour of scat	Collection date	Location	Scat contents
2 black	6 Jan	76.98° S, 155.42° W[a]	57 otoliths, *P.a.*
6 black	9 Jan	74.41° S, 135.67° W	5 beaks, *P.g.*; 253 otoliths, *P.a.*
10 green	13 Jan	73.25° S, 131.88° W	No items
2 black	16 Jan	73.08° S, 129.91° W	3 beaks, *P.g.*; 1 otolith
1 brick-red	19 Jan	69.87° S, 135.28° W	6 otoliths, *P.a.*; fish bones
1 red	21 Jan	67.75° S, 138.97° W	Chitin; *Esirus*[b]
4 red/brown	23 Jan	69.66° S, 143.88° W	Chitin; *Euphausia* eyes; fish bones; 1 beak
1 black	24 Jan	71.22° S, 142.11° W	Eye stalks; 8 otoliths
8 brown	25 Jan	72.00° S, 140.00° W	Chitin; worms
6 black	28 Jan	75.02° S, 145.53° W	135 otoliths, *P.a.*; beaks; fish bones
10 red	4 Feb	73.88° S, 157.93° W	Chitin; 1 otolith

[a]Fast ice edge
[b]Divers saw a swarm of the amphipod *Esirus* spp. under an ice floe near this collection site

or along the narrow shelf slope (Fig. 1). Black scats were found at 6 offshore locations, with 1 exception along the most eastern part of the track. Otherwise, all scats recorded away from the shelf were red, indicating that the primary food was krill. Based on the distance between the eyestalks and size of the carapace, the species of krill was most likely *Euphausia superba*.

Body mass

The average body mass of 11 pre-moult birds was 32.1 kg, and the average mass of the 18 post-moult birds was 20.3 kg (Table 2). The difference between these means was highly significant ($p < 0.005$) after using a *t*-test for 2 means with unequal variances. The fact that the variance for the premoult birds was larger than the variance for post-moult birds probably indicates that in choosing pre-moult birds, we selected birds in different stages of the pre-moult, some just beginning and some many days from the start of moult. Thus, those selected had been fasting for different periods of time. All were very strong and struggled vigorously until hooded, harnessed, and raised clear of the snow.

The small variance in the mass of the post-moult birds probably indicates a common minimum weight level that these birds can reach and still survive. Loosely attached patches of old feathers indicated that 7 of these birds had not yet entered the water since moulting. All of these birds were weak and did not resist being hooded, harnessed, and weighed.

Table 2. *Aptenodytes forsteri.* Body mass of emperor penguins in January 2000

Date	Location	Mass (kg)
Pre-moult		
3 Jan	75.64° S, 158.26° W	39.0
6 Jan	76.98° S, 155.43° W	35.0
		31.6
		25.5
		28.5
		29.5
10 Jan	74.78° S, 140.73° W	27.0
		36.2
		29.3
		34.4
		37.5
Mean ± SD		32.1 ± 4.52
Post-moult		
20 Jan	64.78° S, 137.32° W	20.5[a]
28 Jan	75.02° S, 145.53° W	18.5
		18.5[a]
		17.5[a]
		16.5[a]
		20.5[a]
		20.0[a,b]
		22.0[a]
2 Feb	70.5° S, 153.57° W	21.5
		23.5
4 Feb	73.89° S, 157.90° W	18.4
		21.5
		20.0
6 Feb	75.18° S, 156.05° W	20.5
		21.5
		17.3
		23.0
		24.0
Mean ± SD		20.3 ± 2.17

[a]Some old feathers still attached and evidence that the bird had not yet entered the water since moult
[b]Platform transmitter terminal (PTT) 6256 attached

Movements of satellite tagged birds

Tables 3 & 4 summarize the data on longevity of PTTs and movements of instrumented birds. PTTs 18901 and 18902 transmitted for 132 and 133 d, respectively, before ceasing transmission ca. 1 mo short of the calculated duration, based on transmission power, type of batteries, and the estimated cold exposure. Five transmitters that were expected to transmit for a minimum of 84 d lasted for 15, 16, 24, 60, and 83 d (Table 3). The SWSs were expected to shut the transmitters off whenever they were submerged, and haul-out programming should have shut the transmitters off anytime they were dry for more than 3 h. The combined effect of these 2 added features should have extended the duration of the transmitters considerably, but seemed to have little effect.

The number of Class 1 to 3 locations averaged 5.7 d^{-1} during February for 6 of the 7 birds. Their average distance traveled through February was 20.5 km (Table 4). The adult breeding bird (18902) and the non-breeder (18901) averaged 26.2 and 19.5 km d^{-1}, respectively, during February. In March the number of locations for all birds, except 18901, 18902, and 18903, had diminished to <3 d^{-1}. Birds 18901, 18902, 18903 had from 4 to >9 locations d^{-1}. By April, only Birds 18901 and 18902 were transmitting reliably.

The 4 birds with the shortest duration tracks remained in the eastern Ross Sea and off the continental shelf, well within the pack ice. All moved west. The last transmission of the most northerly bird (6286) occurred 21 February at 73.8° S. The last transmission from the most southerly bird (16260) was on 4 April at 77.3° S, over the continental shelf near Cape Colbeck (Fig. 4a).

The track of 18901, a non-breeder (Fig. 4b), is interesting for several reasons. It was captured well north of

Table 3. *Aptenodytes forsteri.* Summary of data on birds monitored from January to February 2000. SWS: salt-water switch (see 'Materials and methods')

Bird ID	Release location	Start	End	Days	Body mass (kg)
6256; SWS	75.20° S, 145.53° W	28 Jan	14 Mar	15	20
6286; SWS	74.63° S, 156.46° W	5 Feb	21 Feb	16	21.5
6287; SWS	74.97° S, 157.04° W	6 Feb	1 Mar	24	23
16260; SWS	73.88° S, 157.93° W	4 Feb	4 Apr	60	28.5
18901; SWS	73.97° S, 147.63° W	29 Jan	9 Jun	132	23
18902	73.88° S, 157.93° W	4 Feb	16 Jun	133	23.5
18903; SWS	73.97° S, 147.63° W	29 Jan	23 Apr	83	21

the shelf on 29 January (Table 3). Over the next weeks it traveled south to the shelf slope and then west, paralleling the coast near the shelf slope and pausing north of Cape Colbeck until mid-April, when it was over the abyssal plain side of the shelf slope. From mid-April and through most of May it then moved rapidly, almost directly north to ca. 70.5° S, where it remained until the transmitter stopped. The direct-line distance was 670 km, whereas the total meandering distance was ca. 2040 km. By this time (9 June), the sun had set, the brightest sky was 4 h of civil twilight, and it was 132 d since deployment of the transmitter.

The second detailed track is that of putative breeding bird 18903 (Fig. 4b). It was released on 29 January (Table 3), at the same time and place as 18901, and locations were first determined on 2 February. Throughout February this bird remained off the continental shelf, moving quickly at a rate of ca. 28.8 km d^{-1} (Table 4) to the west while following the 74th parallel. Through March, it traveled south and west at 38.2 km d^{-1}. Within 2 wk it had crossed the shelf slope, and by 3 April it was at a longitude of ca. 175° E. It remained over the continental shelf as it traveled north. The last transmission was on 23 April, at ca. 73.4° S, 83 d from the time of deployment.

Breeding bird 18902, which was released on the same day as 16260, moved eastward near the 74th parallel for 1 wk (Fig. 4b), and then westward near 74° S at a rate of 26.2 km d^{-1} until the end of February. In early March, after having traveled north for the first week, 18 902 traveled southwest at 34.4 km d^{-1}, crossed the shelf slope by 18 March, and proceeded to 77.8° S before turning northwest on 24 March. By 15 April it arrived at the Cape Roget colony, where it remained until 16 June when transmissions ceased after 133 d of high quality geographic locations.

Table 4. *Aptenodytes forsteri.* Satellite location data (daily means). Mean distance calculated from the first fix of a series of locations after a long interval (ca. 6 to 10 h) without reception

Bird ID	Month	Locations (no. d^{-1})	Distance (km d^{-1})
6256	Feb	1.1	14.1
	Mar	2.7	24.4
6286[a]	Feb	–	–
6287[b]	Feb	1.5	13.4
16260[c]	Feb	5.9	20.7
18901[d]	Feb	11.6	19.5
	Mar	9.3	24.9
	Apr	4.6	16.8
	May	3.6	17.5
	Jun	1.6	9.9
18902[e]	Feb	6.8	26.2
	Mar	8.5	34.4
	Apr	6.3	40.7
18903[f]	Feb	7.0	28.8
	Mar	4.2	38.2
Mean	Feb	5.7	20.5
	Mar	6.2	30.5
	Apr	5.5	28.8

[a]Data only for Days 5, 6 and 21
[b]One location in March not included in monthly mean
[c]Four locations in March and 1 in April not included in monthly mean
[d]Possible breeder
[e]Breeder
[f]Non-breeder; 1 location in April not included in monthly mean

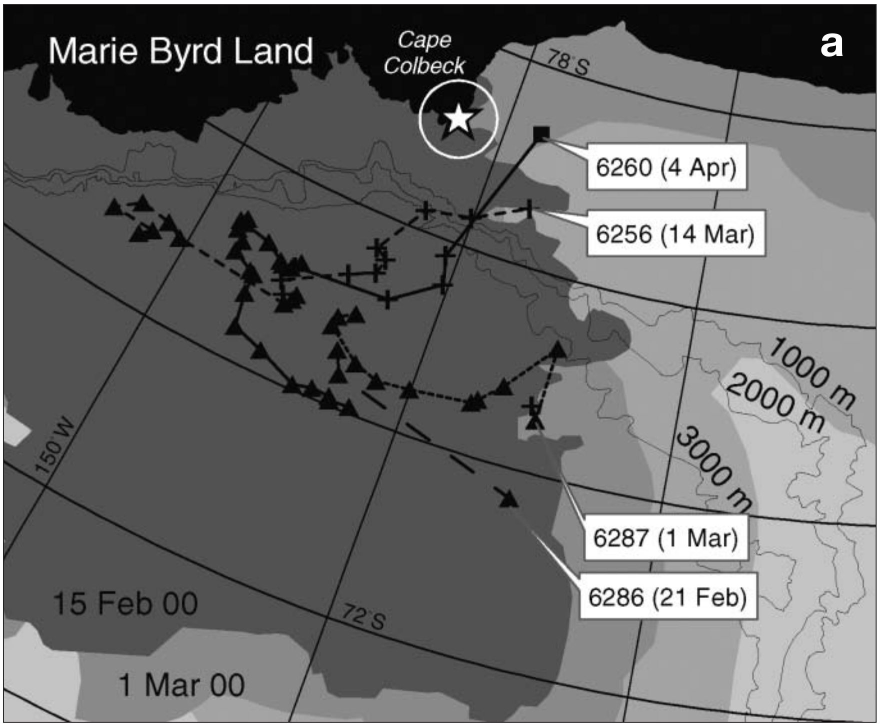
DISCUSSION

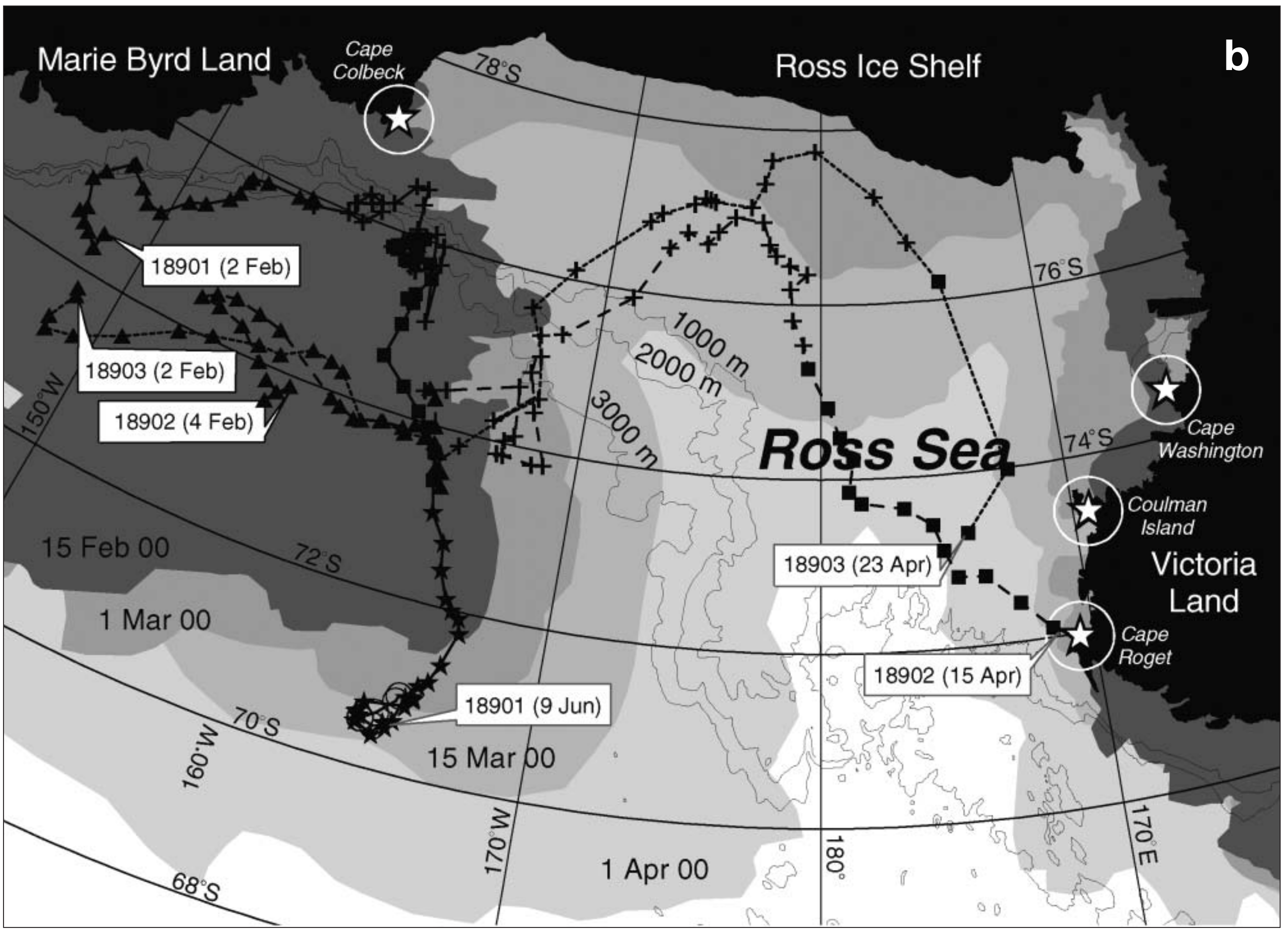
The 1999–2000 cruise of the NBP was the most extensive survey of vertebrates ever undertaken in the eastern Ross Sea since expeditions in the 1980s (Ainley et al. 1984, Ackley et al. 2003) (Fig. 1). In addition, many helicopter transects extended out from the cruise track. We anticipated finding large numbers of emperor penguins in the area because of the results from the satellite tracking of breeding birds from 4 of the 6 western Ross Sea emperor penguin colonies (Kooyman et al. 2000). During the cruise, ca. 11 000 emperor penguins were counted, second only to the count of 16 231 crabeater seals (Ackley et al. 2003).

Sea ice

Missing from the previous telemetry study, which established where emperor penguins traveled in the Ross Sea, was visual confirmation on the ice conditions in the pack ice during the period of residence by the moulting birds. In the Weddell Sea, Kooyman et al.

Fig. 4. *Aptenodytes forsteri.* Movements of 7 emperor penguins in the Ross Sea, monitored by satellite from 1 February to 9 June 2000. (a) Birds 6256 (- - -), 6260 (——), 6286 (– – –), and 6287 (·····); monitoring began between 4 and 6 February 2000, final location noted by date. (b) Birds 18901(——), a non-breeding bird; 18903 (- - - - -), a probable breeding bird whose track ended before reaching a colony in the western Ross Sea; and 18902 (– – –), a breeding bird that returned to the Cape Roget colony on 15 April 2000. Months: February (▲), March (+), April (■), May (★), June (○). Sea ice data were provided by the US National Ice Center. ☆: largest emperor penguin colonies in the Ross Sea





(2000) noted small groups of birds on annual ice floes with dimensions of ca. 100 to 2000 m in width and length, with extensive ridging. During the approximately 30 d moult (Adams & Brown 1990, Williams 1995), birds must not enter the water because in this transitional state their old and new feathers are not waterproof. Without waterproofing, the feathers would become waterlogged, thermal conduction would be excessive, hypothermia would result, and death would probably follow. Therefore, it is essential that the birds select ice floes that remain intact through this period of time.

Pack ice coverage in the eastern Ross Sea declines substantially from late December through February (Fig. 2). Even late in the summer huge floes were still intact in the eastern Ross Sea. Birds that have developed seasonal fidelity to the deep pack ice of this area have a high probability of a stable floe for the duration of the moult. Additionally, many birds were moulting on extensive fast ice adjacent to the shore of Marie Byrd Land (Fig. 1).

Body mass

The bird with the lowest body mass (16.5 kg; Table 2) would probably have to begin feeding within a few days or it would no longer be strong enough to forage. After this time it would simply die of starvation. This seems a narrow margin of safety for a life threatening condition, and implies that emperor penguins are especially sensitive to some kinds of environmental changes during moult. Small perturbations of environmental conditions and/or prey availability could result in a mass mortality in the affected areas.

Diet

It is not surprising that our perception of the postmoult birds we weighed was that they were weak and easily handled. Considering their low body masses, they had lost considerable muscle mass. The relatively large proportion of light-weight birds (<20 kg) in our small sample-size collected randomly from birds near the fast ice edge and the edge of the large floes (Table 2) suggests that many, if not most, birds reach this condition by the end of the moult. It is likely that because the birds decline to a state of such low muscle mass, it is critical that the prey is abundant nearby and easy to catch, so that in the first days after moult they do not have to dive long or deep. For those feeding off the shelf krill was available (Ackley et al. 2003). Adult *Euphausia superba* swarm occasionally near the surface at this time of year (Quetin pers. obs.) when adult krill are accumulating lipids (Hagen et al. 2001), which would make them an ideal prey for nearly starved predators that must replace their body reserves rapidly.

Post-moult travel

Immediately after moulting, the birds must return to the sea, which can be a walk of a few km if the bird moulted on one of the very large ice floes, or perhaps 10 to 30 km if the bird was resident on fast-ice near the continent. Finding a rich food source is the preeminent task at the start of diving. For the bird (18 902) that traveled to the Cape Roget colony, this was a direct distance of 1040 km across the Ross Sea (Fig. 4b). However, the actual distance was a minimum of 2140 km, as estimated from the route taken by the bird. While foraging and fattening in preparation for the winter fast, the bird moved west during February (26 km d^{-1}), and southwest until the end of March (34 km d^{-1}). For the first 2 wk of April it moved directly and rapidly to the colony at Cape Roget (41 km d^{-1}). Although the track is more fragmented, the similarity in the route and rate of travel of Bird 18903 suggests that it was also a breeding bird. However, the transmitter failed on this bird before it reached a colony (Fig. 4b). As the birds moved west, they always remained south of the pack ice edge, which by March was expanding northwards (Fig. 4a,b). During this time, both birds always had several hours of daylight in which to forage. An earlier report of emperor penguins feeding in winter showed that they do not dive during dark periods beyond civil twilight (Kirkwood & Robertson 1997b).

Both birds (18902, 18903) had moved onto the continental shelf by mid-March (Fig. 4b). Prior to that time, we concluded that the main part of the diet was krill and, after moving onto the shelf, we suspect the diet would have changed to fish, primarily the Antarctic silverfish *Pleuragramma antarcticum*. This is the same prey on which they feed while foraging from the colonies in the western Ross Sea (Cherel & Kooyman 1998). It is important to note that in order to support an invasion of ca. 100 000 emperor penguins moving west across the Ross Sea, prey biomass would have to be substantial. From coarse calculations we estimate, with the inclusive assumptions of 15% intake for a body mass of 30 kg, that each bird will consume 4.5 kg of prey d^{-1}. Therefore, 100 000 birds will consume 450 000 kg d^{-1}. If this estimate is assumed for the period of travel from March through mid-April (45 d), then total prey consumed would be 20 250 t.

If we consider the route and behaviour of Bird 18 901 as an example of most non-breeders, then they tend not to travel as fast or as far to the west. The direct distance from the release location to the final location was only 670 km, but the total distance traveled to that point was 2040 km. This does not include the vertical travel distance while diving. The travel rate is ca. 20 km d^{-1} compared to 25 to 40 km d^{-1} for the breeders (Table 4). For the first 2.5 mo, non-breeders remain near the shelf slope, deep in the pack ice (Fig. 4a). The diet near the shelf slope is probably more varied, as they catch fish over the shelf, and krill off the shelf (Fig. 1). By mid-April, when the duration of daylight diminishes to 7 h at 76° S, Bird 18901 traveled almost due north from this time until reaching ca. 70.5° S at a travel rate that declined to <10 km d^{-1} in June. There it remained, and by 9 June, when the last signal was received, the sun had set for the winter and civil twilight lasted ca. 4 h. According the results of Kirkwood & Robertson (1997b), the foraging of emperor penguins during the winter only occurs in the daytime and during civil twilight. Therefore, it would only be during this short period of time that this bird would be likely to forage.

SUMMARY AND CONCLUSIONS

The abundance of large, stable ice floes in the eastern Ross Sea provides a more secure habitat through the month-long moulting period in summer than any other region of comparable distance from the colonies. Weights obtained on pre- and post-moult birds suggest that they are severely stressed energetically at the completion of moult, and require an abundant and accessible food source in the pack ice where moulting takes place. From analyses of scats, it appeared that birds feeding offshore from the continental shelf relied mainly on krill. Birds feeding over the continental shelf fed on squid and fish. Based on a single, complete track it appears that after moulting, breeding birds do not travel directly to the colonies. Instead they travel southwest and remain within pack ice before turning north after the sea ice expands to the north. From another track it appears that non-breeders may stay in the pack further offshore from the colonies and move north to where there may be more light to aid feeding in mid-winter.

In a recent paper about the long-term population variations in an emperor penguin colony at Pointe Géologie, Antarctica, Barbraud & Weimerskirch (2001) note; (1) decreased krill associated with less winter sea ice, and (2) decreased adult survival during warm water events. They comment that it is not known whether the effect is greatest in winter or summer. We propose that during the summer, emperor penguins are at greatest risk. At this time there are at least 2 critical aspects to their ecology: (1) access to large stable floes that will not break up prior to the completed moult, and (2) an abundant food supply accessible immediately post-moult when their body mass is critically low. Any significant reduction in either of those 2 components in the eastern Ross Sea could be a significant detriment to the survival of the birds, and more critical than similar factors at other times of the year. Warm water would be especially detrimental to the needs of emperor penguins during summer. For example, if sea ice at the colony during the fall arrival is not yet adequately formed to facilitate breeding, it could be postponed for days or weeks, or, at worst, the birds might skip a breeding year. Similarly, if prey is insufficient near the breeding colony to successfully raise the chicks to the proper body mass before fledging, then chick production may fail that year. However, for a k-selected long-lived species like the emperor penguin, these problems, local to the colony, are minor for the adults, compared to those they face in the eastern Ross Sea.

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