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Emperor Penguin ***(Aptenodytes forsteri)*** foraging ecology

Roger Kirkwood

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A POME BOUT EM-PRAR PENGWINS

by John Innis.

The biggest penguins on the earth
are Emperors, of noble birth.
They choose to live (with common sense)
south of the Antarctic confluence.
In autumn days, the penguins mate,
the father has to incubate.
They nest on ice and balance eggs
between their scaly little legs.
The mothers don't wait for the hatch,
they have bigger fish to catch.
They walk to sea, to eat their fill
of ice-edge fish, and squid and krill.
The fathers, when a blizzard comes,
will huddle-up next to their chums.
They face Antarctic ice and snows
and keep their children on their toes.
Then mum returns and has to find,
her mate from thousands of their kind.
By trumpet call true love is found,
they know each other by their sound
Together, penguin mum and dad,
will bring up every lass and lad.
(It's part of every pengie pledge,
to stay until the chick can fledge.)
Amazing yes, you would agree,
These penguins from the frozen sea.

Abstract

1. This research investigated the foraging ecology of breeding emperor penguins (*Aptenodytes forsteri*), to better understand the trophic relationships of this seabird in Antarctic marine ecosystems. The study was conducted in 1993 at two Mawson Coast colonies, Auster and Taylor Glacier. I assessed the foraging location, diving behaviour, diet, feeding rates and foraging trip durations of the penguins during the incubation and chick rearing periods of their annual breeding cycle. To complement these studies, I determined the population size and breeding success of the penguins, their energy assimilation efficiency when consuming Antarctic krill (*Euphausia superba*), and their huddling behaviour during foraging trips.
2. At Auster in 1993, about 13,300 breeding pairs of emperors raised 11,156 chicks to pre-fledging age, a breeding success of 84%. At Taylor Glacier about 2400 breeding pairs raised 2015 chicks also a a breeding success of 84%. Compared with previous years, 1993 appears to have been a good year for the penguins — though a critical period took place during September, when about 55% of the mortalities from the whole breeding season occurred.
3. To enable calculations of prey consumption rates, I determined experimentally the emperors' ability to assimilate energy from a krill diet. Captive penguins hand-fed Antarctic krill assimilated an average of 70.5% ± 1.7% (n = 3) of the energy in the diet. The penguins' water intake estimated by tritiated water turnover was 9.4% ± 2.4% less than that measured gravimetrically. In conjunction with the assimilation efficiency experiment, an evaluation of tritium equilibration times found that tritium took 1.5 hours after injection to equilibrate with the penguins' body water pools.
4. Between late May and early August, male emperors remain at the colonies to incubate eggs and females forage at sea for self maintenance. During this time, two satellite-tracked females from Auster foraged about 100 km north-east of the colony in open water over the outer continental shelf and shelf slope where water depths ranged between 200-500 m. Ten Auster and four Taylor Glacier females that carried time-depth recorders took about 8 days to reach the ice-edge, spent 50-60 days at sea foraging and took 4 days to return across the fast-ice to the colony. The females occasionally huddled together to minimise heat loss while in transit to the ice-edge and between foraging days. The penguins foraged on 93.2% of their days at sea and rested for the remainder. On each foraging day, penguins usually entered the water just after dawn and averaged 4.71 hours in the water before exiting at dusk. Hourly dive rate was constant throughout winter but daily dive rate increased as day length increased, suggesting day length is a primary determinant of hunting effort. Penguins exhibited behaviour indicative of feeding on 47% of dives, the remainder being travel or search dives. Penguins made on average 26 feeding dives per day. Females from Auster targeted prey at water depths of 20-70 m and 100-150 m whereas Taylor Glacier birds targeted prey at 10-70 m, 250-300 m and 330-400 m, suggesting between-colony differences in prey distribution.

The stomach contents of 17 females, returning to Auster in July/August to brood their chicks, was dominated by two pelagic prey species, antarctic krill (70% by mass) and antarctic silverfish (*Pleuragramma antarcticum*, 13% by mass). Food consumption rates during winter for five penguins from both colonies were similar and averaged 62.6 ± 5.8 g/kg·d^{-1} (1.8 ± 0.1 kg/d for a 28.8 kg female) which equated to a metabolisable energy intake of 236.6 ± 22.0 kJ/kg for each day they foraged; this enabled the birds to gain about 6.1 kg for a trip spaning about 70 days. Based on mean prey masses and the penguins' dive rates, the penguins were estimated to have consumed about 115 x 0.6 g krill or 16 x 4.3 g antarctic silverfish per foraging dive, or some combination of both. In their winter trip, each breeding female consumed about 100 kg of prey. The breeding females from Auster and Taylor Glacier colonies consumed an estimated 1350 metric tons and 250 metric tons of prey, respectively, during winter.

5. Chicks hatched in late winter when day lengths started to increase. Stimulated by the requirements of the growing chicks, and facilitated by the increasing day lengths, the daily swimming time of the penguins' while on foraging trips increased from the females' winter rate of about 4.41 hours to 7.83 ± 1.50 hours in August, 12.23 ± 1.25 hours in September, and 12.95 ± 1.24 hours in October. Accordingly, the penguins' dive rate increased to 92.7 ± 28.5 dives/d, 149.4 ± 23.4 dives/day, and 161.6 ± 19.3 dives/day, in the respective months. The birds targeted prey in the vicinity of the continental slope mainly at depths <100 m, although some individuals frequently hunted at depths >200 m and the maximum depth measured was 438 m. Overall, Antarctic krill was the most common prey taken, averaging 41% of the diet by mass, and dominating the diets between August and October. The contribution of krill to the diet reduced over time from 68% in August to just 1% in early December. In November, the glacier squid (*Psychroteuthis glacialis*) dominated the diet (47-63%), and in early December the diet comprised various species of fish (*Trematomus* sp. [27%], *Pagothenia borchgrevinki* [24%], Antarctic silverfish [8%]), and squid (glacier squid [13%], and *Alluroteuthis antarcticus* [9%]). The birds' prey consumption rates more than doubled between late winter and early summer, from 4.0 ± 1.0 kg/d to 8.7 ± 1.7 kg per foraging day. These values are equivalent to metabolisable energy intakes of 628 ± 134 kJ/kg·d^{-1} and 1422 ± 308 kJ/kg·d^{-1}, respectively. During brooding (late winter–early spring), female trip durations were shorter than the those of the males (8.7 ± 2.7 days versus 17.7 ± 3.8 d). Thereafter trip durations of both sexes were similar and declined from 15–19 days in spring, to <10 days in early summer. Between hatching and about one week prior to fledging each parent fed its chick seven or eight times. While raising a chick, females and males consumed about 410 kg and about 470 kg of prey respectively, or about 880 kg for each breeding pair. Seasonal variations in the penguins' foraging were probably influenced by fluctuating sea-ice conditions, differences in the prey types available, changes in day-length toward summer, and increasing demands of the growing chicks.

6. In addition to assessing the penguins' behaviour in the water, I investigated their behaviour out of the water during foraging trips. Between May and October 1993, temperature/light recorders mounted on the backs of penguins on foraging trips recorded occasions when light intensities were consistent with night-time but temperatures exceeded 23°C (the upper limit of the sensors); ambient air temperatures were <-15°C. The most likely explanation for the low light and high temperatures is that the penguins huddled together to share body warmth. The penguins apparently huddled at night during journeys to and from the ice-edge, especially on arrival at the ice-edge, and occasionally between foraging days at sea. Between June and October, as day length and ambient temperatures increased, the frequency and duration of huddling events decreased. Away-from-colony huddling would reduce a penguin's metabolic costs while resting on the sea ice during cold periods, and could reinforce a behaviour that is required to survive extended periods of fasting at the colony.
7. Emperor penguins are opportunistic foragers that exhibit substantial temporal, spatial and individual variation in their foraging patterns. They feed primarily on pelagic species (krill, Antarctic silverfish and glacier squid), but at times feed on benthopelagic species, like *Trematomus* sp.. The emperor penguin is the largest seabird species, the only higher consumer to breed in Antarctica during winter, and a major consumer of a variety of antarctic marine resources, making it a key species for antarctic ecosystems research.

Preface

This report is compiled as a series of papers (Kirkwood and Robertson 1997 a, b, c and 1999), and as such, Chapters 3 to 6 are self-contained; there is some descriptive repetition between these chapters. The papers from these chapters are co-authored with Graham Robertson, a supervisor and my employer during the data collection. In all the papers, I was the senior author, and was responsible for pre-trip planning, data collection in the field, data analysis and preparation of the publications.

This research was restricted by several factors related to field-work in Antarctica. Ecological research often incorporates manipulative experiments, which are important to the understanding of aspects of functional ecology.

When studying populations of small animals in a temperate environment manipulative experiments can incorporate large sample sizes and controls. However, in the antarctic environment when studying 30 kg birds that demand respect, manipulative experiments are difficult, and sample sizes are necessarily small (see Chapter 3).

Conducting field research on higher predators in Antarctica requires extensive logistical support which, at times, can constrain the research. Due to the considerable resources required to support sea-ice based research from an isolated field camp during the antarctic winter, spring and summer, data collection for this thesis had to come from a single year. Consequently, important ecological comparisons, for example those related to interannual variability, were constrained in the present study. During the year in Antarctica the opportunity to modify or repair equipment was limited and new equipment could not be installed, so failed projects could not be repeated.

Finally, all aspects of the study required prior approval from an ethics committee, and the permits subsequently issued stipulated numbers of penguins and times when they could be handled; there was limited scope for modifying the project during its implementation. Despite the restrictions, this research provided a rare opportunity for a comprehensive study of the foraging ecology of emperor penguins during an entire breeding season.

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1. GENERAL INTRODUCTION

1.1 Introduction

A prerequisite for being able to manage and protect complex ecosystems that are affected by human activities, is to understand the trophic relationships and foraging ecology of the main species within the systems. In polar ecosystems, direct human activity, such as mining, fisheries and tourism, and indirect human activity, such as altering global climate, have the potential to cause irreversible damage at the ecosystem level. Antarctic waters are currently fished for krill, fish and squid species (Koch 1992, CCAMLR 1996), and these activities pose real threats to the stability of antarctic marine ecosystems. It is quite possible that overexploitation of whales, seals and some fish species in antarctic waters has already modified the antarctic ecosystem (May 1989). It is difficult to determine the precise nature and extent of the changes this overexploitation has caused because the ecosystems were poorly understood before major fishing began (Agnew and Nicol 1996), and there remains a dearth of information on antarctic marine ecosystems. Future changes to these ecosystems will be difficult to predict and assess unless more knowledge is gained concerning the ecology and associated trophic relationships of the main species present.

In this study, I investigate the foraging ecology of the emperor penguin (*Aptenodytes forsteri*), one of the most abundant higher predators in antarctic waters (e.g. Woehler 1993). The foraging capacity and reproductive success of the emperor penguin, as with all higher predators, provides an indication of the productivity of the ecosystem in which it lives (Croxall and Lishman 1990). Studies of the diet of emperor penguins (Offredo and Ridoux 1986, Klages 1989) suggest the penguins may rely heavily on pelagic prey that are or could be targeted by commercial fisheries, and information on the emperors' current foraging ecology is needed to better assess the affects of future human impacts on the penguins' environment.

The general aims of this study are to assess the population status, foraging areas, foraging behaviour, diet, and consumption rates of emperor penguins from two colonies on the Mawson Coast of Antarctica, between May and December 1993. But before addressing these aims, it is valuable to consider the broad role of seabirds as marine predators, and to review our current understanding of the biology of emperor penguins and the environment in which they forage.

1.2 Seabirds as marine predators

Seabirds are a specialised group of birds that breed in coastal environments and derive all their food and energy from the sea (Whittow and Rahn 1983). Seabirds possess several common features. For instance, their diet comprises mainly small bodied pelagic fish, squid and crustacea that are variable both in distribution and abundance (Montevecchi 1993). In addition, to sustain their populations in environments of fluctuating resources, seabirds have evolved extreme K-selected life-history strategies (Furness and Monaghan 1987), which means they are generally large in body size, exhibit a delayed maturity, have low annual reproductive outputs and low adult mortality rates (Croxall 1984). Other common features of seabirds include their propensity for breeding in stable, crowded populations or colonies (Horn and Rubenstein 1984), and their ability to forage at great distances from their breeding sites. The availability of suitable nesting habitat and the productivity of accessible ocean regions determines seabird distributions and population sizes (Ashmole 1963, 1971, Lack 1966, Diamond 1978, Croxall and Prince 1980). Because of their broad distribution and large biomass, their consumption of a variety of prey, and their necessity to return to predictable breeding sites, seabirds provide a useful means of measuring changes in marine resources (Cairns 1987, Le Maho et al. 1993, Cherel and Weimerskirch 1995).

Seabirds concentrate their foraging effort where prey are most available to them, such as in regions where water bodies converge or where bottom topography induces the up-welling of nutrients, as occurs over sea-mounts (Haney et al. 1995) or continental shelf breaks (Brown 1980, Hunt and Schneider 1987, Plötz et al. 1991). Within such regions, prey availability to avian predators varies spatially and temporally. Spacial variation can be dependant on habitat modifiers, including eddies, wind rows and tidal boundaries (Ainley and Jacobs 1981, Ainley et al. 1995), while temporal variation may be influenced by seasonal changes in habitat (Ainley et al. 1986, Fraser and Trivelpiece 1996), as well as prey breeding cycles and migratory patterns (Fraser et al. 1989, Daly and Macauley 1991). Seabirds appear to allocate their foraging effort between searching for prey patches, with occasional feeding, and periods of intensive feeding once prey patches are located (Naito et al. 1990, Wilson 1995). This strategy probably enables the birds to forage most efficiently.

1.3 Penguins

Penguins (Order Spheniscidae) are perhaps the most specialised of seabirds (Williams 1995). Historically, penguins probably originated in the region of New Zealand, but now their greatest populations are in the Southern Ocean (Fordyce and Jones 1990). They breed in extremely harsh terrestrial environments and display profound adaptations to the marine environment, including the loss of aerial flight, high body density and extreme hydrodynamic shape (Whittow and Rahn 1983, Croxall and Lishman 1990). All species of penguins reside in the Southern Hemisphere where their characteristic large body sizes (1–40 kg) and enormous populations (totalling >30 million breeding pairs, Woehler 1995) make them a significant biomass of consumers of marine resources (Croxall 1984, Williams 1995).

Penguins feed on live prey which they hunt in water depths ranging from near the surface to >500 m (Kooyman and Kooyman 1995). Their foraging ranges, although poorly understood, are apparently very diverse between species. Some species, for example, are resident and forage year-round in the vicinity of their breeding sites, while others undergo annual migrations and may forage thousands of kilometres from their breeding sites (Wilson 1995).

Breeding by penguins inhabiting the Southern Ocean is restricted to the isolated Subantarctic islands and coastal areas of the Antarctic continent. The extreme cold experienced in winter at these breeding sites generally forces penguins to breed during summer months (e.g. Ainley et al. 1983), although an exception to this pattern is exhibited by the two species of the genera *Aptenodytes*. King penguins (*A. patagonicus*) breed on Subantarctic islands and require 11–13 months to complete a breeding cycle, and emperor penguins (*A. forsteri*) breed around the Antarctic continent and have a 9 month breeding period that extends from late autumn to early summer (Stonehouse 1960, Prévost 1961).

1.4 Emperor penguins

1.4.1 Distribution and abundance

Emperor penguins live year round in antarctic waters and have a circumpolar distribution (Watson 1975). They breed at 30 known colony sites with an estimated total population of 200 000 breeding pairs (Woehler 1993). Most colonies are located between 20°W and 110°E along the coast of East Antarctica, although there is a concentration of approximately 80 000 breeding pairs at six colonies in the Ross Sea Sector of East Antarctica (160°E to 170°E; Harper et al. 1984). The latitudes of colonies range from 66°S to 78°S. Typically, emperor penguin colonies are located on the antarctic fast ice in areas where the ice forms earliest in the year and remains stable from winter to early summer. Two colonies are on land, however; one on Dion Island near the Antarctic Peninsula (67°52'S, 68°43'W) and the other, the only colony on the Antarctic continent, is beside Taylor Glacier (67°28'S, 60°53'E) in MacRobertson Land.

1.4.2 General biology

Emperor penguins are the largest seabird, standing 115 cm tall and weighing up to 40 kg (Marchant and Higgins 1990). Their size provides them with a low surface-to-volume ratio and sufficient thermal mass to survive both extreme cold (<-40°C temperatures) and extended periods of fasting (up to five months; Le Maho and Delclitte 1974). Of all antarctic seabirds, emperor penguins have adapted the best to the cold conditions, and they are the only seabirds capable of breeding during winter in the high Antarctic (south of 66°S; Le Maho 1977).

Emperor penguins possess a number of highly developed physiological and behavioural adaptations to cold compared with other penguins (Le Maho 1977, Le Maho et al. 1981). For example, the emperor penguin has smaller extremities relative to body size than do other penguins (Stonehouse 1967), the heat-conservation, counter-current system in their brachial arteries is twice as extensive as that of the king penguin (Trawa 1970), and the density of the emperor's plumage, which provides approximately 85% of the bird's insulation, is greater than that of other penguin species (Bougaeff 1972, 1974). Further to these physiological adaptations, emperor adults exhibit the unique huddling behaviour that allows them to maintain thermoneutrality in cold weather, and reduce their rate of mass lost through heat generation to approximately half that of isolated birds (Prévost and Bourliére 1957, Prévost 1961).

The breeding biology of emperor penguins is summarised below, (Fig1.1) based on studies conducted at Dion Island in 1949 (Stonehouse 1953) and at a colony near Pointe Géologie (66°40'S, 140°01'E) in the 1950's and 60's (Prévost 1953, 1958 and 1961, Mougin 1966, Isenmann 1971, Jouventin 1971). Emperor penguins mature at 4-6 years of age and can live for up to 25 years. In March,

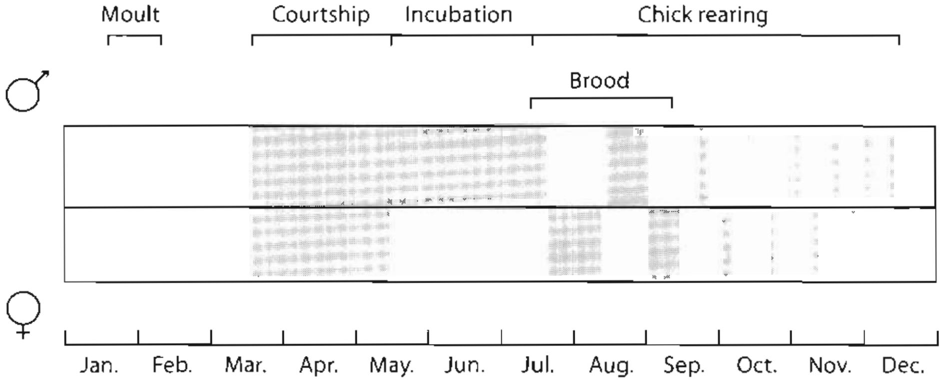


__Figure 1.1__ A stylised diagram of the annual cycle of mature emperor penguins, grey indicating the penguins' attendance at the colony. During moult (hatched), the penguins remain out of the water for approximately three weeks, either at the colony site, or other areas of stable sea-ice or land.

mature birds assemble on the sea ice at their colony sites and commence a 6 week courtship and egg production period (Figure 1.1). The arrival at the colony initiates a two month fast by females and a four month fast by males. Eggs are laid between mid-May and early June. Each female lays a single 450g egg which she passes to the male before departing the colony to forage at sea for the entire 55-65 day incubation period. During incubation, the male carries the egg on his feet, pressed up against a warm brood patch and shielded from the cold by an abdominal skin fold. Over much of this period, the males huddle together to share body warmth and minimise energy expenditure.

Chicks hatch in July and are first fed by the male, who produces a milky secretion from his oesophagus (Prévost and Vilter 1963). Males can feed the chicks with these secretions for up to two weeks. Females return between early July and mid-August. Upon entering the colony, they locate their mates by calling (Isenmann 1971), and take the chick. The male then leaves the colony for a 3 week foraging trip.

Through August and September, the parents take turns to brood the chick while the other forages at sea. During late September, the chicks are 'emancipated' (set free by their parents to defend themselves) and form crèches at the colony while both parents go to sea and forage, returning as often as possible to feed the chick. At emancipation, chicks are about 50 days old and weigh 2–3 kg.

In crèches chicks can huddle tightly for shared warmth, but as the chicks grow and the ambient temperature warms with the approaching summer, the huddles become unnecessary, and after early November the chicks roam the colony as individuals. The chicks begin to moult into juvenile plumage in late November and fledging commences in mid-December, at which time the chicks are about 150 days old and have attained body masses of 10–15 kg, approximately half the mass of the adults (Robertson 1992).

Once their chicks have fledged, the parents are free to forage for themselves and build body mass in preparation for their moulting fast. Adult moult commences in late January and lasts about three weeks. After their moult, the adults again forage at sea and gather energy reserves for their forthcoming breeding season.

1.4.3 Foraging ecology

The foraging ecology of emperor penguins has been investigated in studies of diet (Offredo et al. 1985, Robertson et al. 1994a, Pütz 1995, and references therein), diving physiology (Kooyman et al. 1971, Kooyman et al. 1992), diving behaviour (Ancel et al. 1992, Robertson 1994, Kooyman and Kooyman 1995) and foraging energetics (Robertson and Newgrain 1996). Emperor penguins are versatile hunters and catch prey ranging in size from 1g crustaceans to 500g fish and squid (Klages 1989, Robertson et al. 1994a, Pütz 1995). Emperors can dive for longer durations (up to 22 min, Robertson 1994) and to greater depths (to 534 m, Kooyman and Kooyman 1995) than any other seabird. The emperor's diving capacity enables it to exploit prey from directly beneath the sea ice to near the ocean floor over most of the continental shelf, and out into pack ice and open water regions of the Southern Ocean. Despite the present understanding of the emperor's foraging ecology, important aspects of its foraging remain unknown (Robertson 1994, Kooyman and Kooyman 1995); for example, virtually no studies have investigated the foraging ecology of emperors in winter. Moreover, the foraging ranges, foraging behaviour and temporal and spatial variations in foraging ability are poorly understood. The present study aims to redress some of these gaps in our knowledge.

1.5 The Antarctic marine environment

To place the foraging ecology of emperor penguins into perspective, a general description of the foraging environment is required. Antarctica is a continental landmass situated over the South Pole and surrounded by a broad (up to 100 km) continental shelf. Beyond the continental shelf, is the circumpolar Southern Ocean. This has a breadth of almost 1000 km, extending to the region of the Antarctic Polar Front where the cold antarctic waters interact with warmer subantarctic waters. The Antarctic Polar Front serves as a barrier to the dispersal of marine species and, as a consequence, many species in the Southern Ocean are endemic (e.g. Gon and Heemstra 1990).

The Southern Ocean possesses unique characteristics which distinguish it from other oceans. A dominant ecological factor in the Southern Ocean is the marked seasonality in primary production (Clarke 1988), which is much greater than seasonal variations in primary production in more temperate seas (Cushing 1975). During summer in the Southern Ocean, phytoplankton bloom, whereas in winter both standing crop and primary productivity are low (Whitaker 1982). This seasonality profoundly influences the biology of all consumers in the Southern Ocean, affecting their foraging ecology, breeding chronologies and life-history strategies (J. Kirkwood 1993). The driving force behind all seasonality in the Southern Ocean is the annual fluctuation in incident solar energy (Clarke 1988).

Other prominent features of the Southern Ocean are its huge expanse of cold surface water and its cover of sea ice which fluctuates in area from less than 4 x 10^6 km^2 in summer and up to 20 x 10^6 km^2 during winter (Zwally et al. 1983). The formation of sea ice during winter creates a number of zones in the sea-surface; the coastal fast ice zone, the circum-polar polynya region offshore from the fast ice, the pack ice zone and the ice-free oceanic zone (Eicken 1992). The fast ice, which is attached to the continent, contains ice-free polynyas - regions of open water within the sea ice - that are formed by ice movement around glacier tongues or by increased water temperatures in relation to areas of shallow water or up-welling. The circum-polar polynya at the outer boundary of the fast ice is generated by offshore winds (Zwally et al. 1985). At low temperatures, rapid ice growth can quickly reduce the size of this polynya, but high winds along with wave and current action can also quickly increase the polynya's size. Offshore from the polynya is the zone of highly deformed pack ice which is fed by the advection of broken fast ice across the polynya and incorporates locally formed sea ice (Eicken and Lange 1989). During summer months, the fast ice structure deteriorates, allowing wind and ocean swell to break it up and transport the resulting ice-rafts offshore. The fluctuating sea ice will influence the foraging patterns and life-cycles of all seabirds in Antarctica. It dictates where they can feed and what they can feed on.

Another important feature of the Southern Ocean is its low species diversity, relative to more temperate marine systems (Krebs 1985). The low species diversity contributes to a relatively simple trophic structure which, in antarctic waters, is centred around Antarctic krill (*Euphausia superba*, Laws 1985, Moloney and Ryan 1995, Nicol 1994). Estimates of the biomass of krill range from 100 million to 1.35 billion metric tons (Ross and Quetin 1988, Nicol and de la Mare 1993), and fisheries for krill have landed up to 500 000 tonnes in a single fishing season (CCAMLR 1996). The pivotal position of krill in antarctic marine ecosystems and their potential commercial importance present a major challenge to the conservation and management of the Southern Ocean ecosystems.

A further feature of the antarctic environment that greatly influences the foraging behaviour of antarctic predators is the seasonal fluctuation in day-length. During winter, the sun can remain below the horizon for several months, whereas during summer the reverse is true. Since penguins tend to be daytime foragers (Wilson 1995) and presumably hunt by sight (Wilson et al. 1993), light conditions are likely to impose temporal restrictions on foraging during winter.

1.6 Study site

Field work for this study was conducted at two emperor penguin colonies on the Mawson Coast of MacRobertson Land, East Antarctica. The Mawson Coast faces north and is about 600 km long, its boundaries being the Amery Ice Shelf to the east, and Enderby Land to the west (Figure 1.2). It consists of ice-cliffs separated by glacier tongues and occasional rock outcrops.

The continental shelf in this region is about 100 km wide and generally 100–500 m in water depth, although the sea-floor is dissected by several 1000 m deep marine canyons. Water currents over the continental shelf tend westerly,

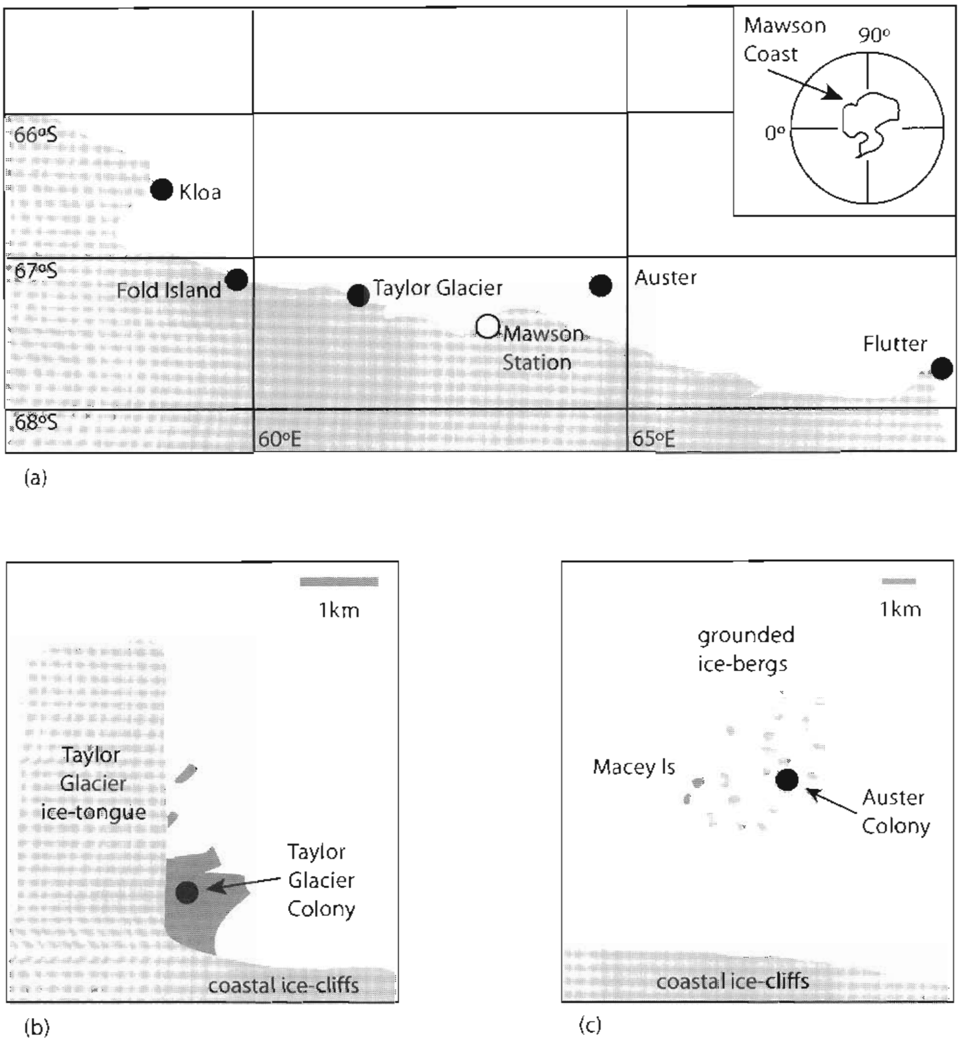


Figure 1.2 *A map of the locations of emperor penguin colonies on the Mawson Coast of Antarctica (a), and details of the terrain around the Taylor Glacier (b) and Auster (c) Colonies.*

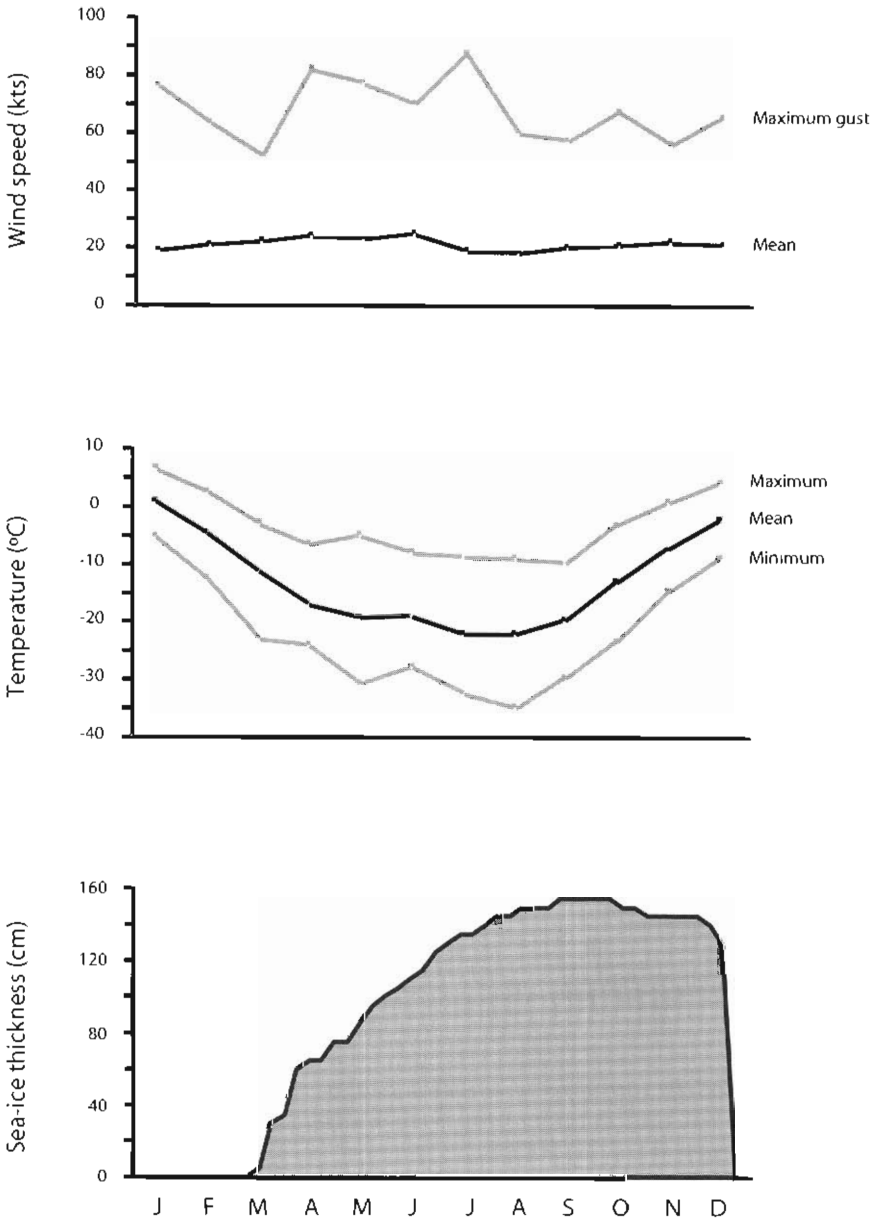
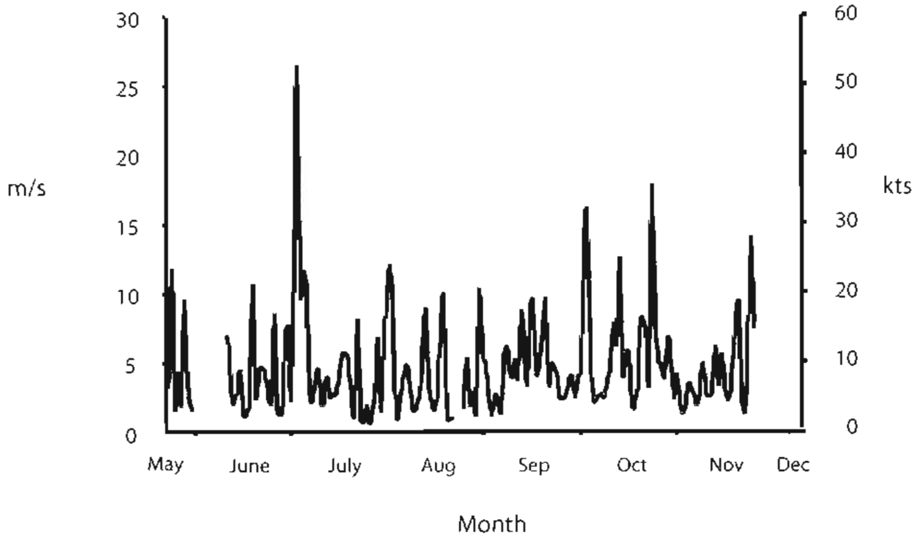


Figure 1.3 *Wind speed, ambient temperature and sea-ice thickness at Mawson Station during 1993 (Data collected by Bureau of Meteorology).*

(a) Wind speed



(b) Wind direction

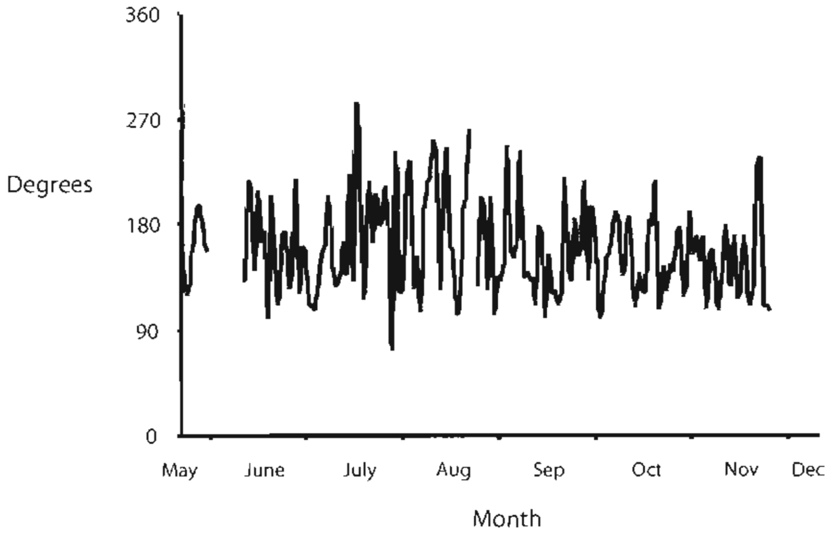


Figure 1.4 *Mean daily wind speed (a) and direction (b) experienced by emperor penguins at Auster Colony during 1993. The wind parameters were measured with a Woeffle Anemometer that was erected 1.0-1.5m above the sea-ice at the colony.*

whereas off the shelf the circumpolar current travels easterly (Deacon 1982, Allison 1989, Nunes Vaz and Lennon 1996).

Emperor penguins breed at five colonies on the Mawson Coast, which from west to east are; Kloa Point (66°38'S, 57°19'E; 2500 breeding pairs), Fold Island (67°20'S, 59°23'S; 1000 pairs), Taylor Glacier (67°28'S, 60°53'E; 3000 pairs), Auster (67°23'S, 64°02'E; 12,000 pairs) and Flutter, at Cape Darnley (67°50'E, 69°45'E; 5000 pairs; Willing 1958, Budd 1961, 1962; Figure 1.2). One-tenth of the total population of emperor penguins breed on the Mawson Coast.

The two colonies studied were at Auster and at Taylor Glacier, which are 15 km offshore and 50 km east, of Mawson Station and on the coast 80 km west of Mawson Station, respectively. A field camp was established on Macey Island, 7 km west of Auster colony (Figure 1.2) and occupied between May and December 1993. From the camp, near-daily visits were conducted to the Auster colony and near-monthly excursions to the Taylor Glacier colony.

Weather on the Mawson Coast is influenced by almost continuous, southerly katabatic winds, and clockwise rotating low-pressure systems that move from the west and south-west (Schwerdtfeger 1970, Streten 1990). The low-pressure systems are regularly projected sea-ward by the landmass of Enderby Land, which has a sheltering effect over the coastline. Katabatic winds from the south and south-east, therefore, constitute the main surface wind pattern. Mean monthly wind speeds recorded at Mawson Station stayed between 20–25 kn throughout 1993 (Bureau of Meteorology; see Figure 1.3). Wind speed and direction experienced by penguins at the Auster colony were monitored with a Woeffle anemometer that was erected 1.0–1.5 m above the ice surface (Figure 1.4). Winds at this location usually came from the south at mean daily speeds that reached 30 m/s: (i.e. 60 kn), but invariably were less than the wind speeds recorded at Mawson. This was probably because Auster is located 15 km from the coast, and away from the effects of katabatic winds (Streten 1990). Mean monthly temperatures recorded at Mawson ranged from 3.9°C in January to –22.1°C in July and August (Figure 1.3). These average winds and temperatures are about average for Mawson compared with previous years (Streten 1968, 1990).

Adjacent to Mawson, fast ice started to form in March 1993 and achieved a maximum thickness of 1.6 m in September, then started to deteriorate until it broke up in mid-December (Figure 1.3).

1.7 Report structure

This chapter provides an introduction to the report. In Chapter 2, I assess the population size and breeding success of the penguins at the two study colonies during 1993. Knowledge of a population size and breeding success is of primary importance to the assessment and quantification of prey requirements of a population, and aids the understanding of the trophic relationships of a species (Croxall et al. 1984, Croxall 1987). As well as determining the population size and breeding success, I monitored the mortality rates of eggs and chicks to determine critical stages during the breeding period that affected overall breeding success.

Calculation of prey consumption rates requires information on the consumer's assimilation efficiency. Previously, Robertson and Newgrain (1992) estimated the assimilation efficiency of emperor penguins fed squid and fish. To complement this earlier research, in Chapter 3 I assess experimentally the ability of emperors to assimilate energy from krill, which is important food for the penguins (Klages 1989 Pütz 1995).

The central component of this report, the investigation of emperor penguin foraging ecology, is presented in two chapters. The first chapter (4), describes the penguins' foraging ecology between May and July/August, the incubation period, when only the females go to sea and the males remain with the eggs at the colony. The second chapter (5) details the foraging behaviour of adults between August and December, the chick rearing period, when both parents attempt to raise the largest chick possible before fledging commences in early summer.

Emperor penguin huddles were first observed in 1911 when an emperor colony was first visited in winter (King 1972) and since then, have been reported only at the colonies. Extensive research by French investigators (e.g. Prévost 1961 Isenmann and Jouventin 1970 Groscolas and Clément 1976 Le Maho et al. 1976 Ancel et al. 1997) has highlighted the energy savings associated with huddling, particularly for the males during winter, which may be critical to the survival of emperors in the harsh antarctic environment. While researching the emperors' foraging ecology with devices attached to the penguins' backs, I obtained records of apparent huddling behaviour away from the colony. Chapter 6 is a specific study of this unusual huddling behaviour, and its potential importance to the penguins.

In a general discussion (Chapter 7), I summarise the main findings of the report and assess the foraging strategies of emperor penguins as seabirds that hunt live prey in the Antarctic marine environment.

Two appendices to the report present studies that were not central to the theme of emperor penguin foraging ecology, but influenced how the research was conducted. Appendix I describes the structure of emperor penguin colonies, and Appendix II describes investigator-induced disturbances and their effects on the penguins.

2. POPULATION SIZE AND BREEDING SUCCESS AT AUSTER AND TAYLOR GLACIER EMPEROR PENGUIN COLONIES

2.1 Introduction

To place the trophic relationships of a species into an ecological perspective, it is important to know the species' population size and breeding success. Knowledge of population size enables an estimation of resource consumption by the population to be extrapolated from the requirements of a representative sample of individuals. How successfully the species exploits its resources can be reflected in its breeding success. In this chapter, I provide estimates of the population size and breeding success of emperor penguins (*Aptenodytes forsteri*) at the Auster and Taylor Glacier colonies during 1993.

Previous counts of emperor penguin population sizes have often been unreliable. Several estimates were based on single visits or over-flights of colonies (e.g. Willing 1958, Budd 1962, Cracknell 1986) and at times, population trends have been inferred from as few as two counts (Yeates 1975). Such inferences ignore the potential for interannual variations in breeding numbers and breeding success (Stonehouse 1964, Jouventin and Weimerskirch 1990). The most comprehensive monitoring of an emperor penguin population size has been conducted at the Pointe Géologie colony in Adélie Land (66°40'S 140°01'E; Prévost 1958, Thomas 1986, Jouventin and Weimerskirch 1990, 1991) where the number of breeding pairs has declined from approximately 6 000 to 2 500 between 1952 and 1987. By contrast, populations on the Mawson Coast appear to have been stable since the 1950 s (Budd 1961, 1962, Robertson 1992).

Estimates of breeding success have received scant attention in previous studies of emperor penguin populations, except for the regular monitoring at Pointe Géologie Colony (Prévost 1958 Thomas 1986 Jouventin and Weimerskirch 1990, 1991). At other colonies, counting failed eggs and chicks has rarely been attempted, because it is labour-intensive and requires regular collections during the penguins' nine month breeding period. On the Mawson Coast, several estimates were recorded from the 1950s (Budd 1961, 1962) and in 1988 (Robertson 1992).

Failure of eggs and chicks may result from infertility, an inability of their parents to provide adequate food and protection, or abiotic factors such as strong winds, ice-falls, or break-up of the sea ice.

Counting techniques at emperor penguin colonies have often been invasive. Emperors carrying eggs or small chicks on their feet cannot move much and may lose their young if disturbed by herding or low flying aircraft, which have been employed in previous population counts (Budd 1962, Hoshiai and Chujo 1976). Some studies have noted high rates of investigator-induced mortality due to regular human visitation (e.g. Kamenev 1968). There is therefore, a need to adopt methods for estimating emperor penguin colony sizes and breeding success that not only take into account the penguins' unique breeding strategy, but also minimise that disturbance. In 1988, estimates of the population size, breeding success and chick mortality rates at Auster and Taylor Glacier were estimated using techniques that appeared to achieve these purposes (Robertson 1992). The present study replicates and further develops the techniques adopted in 1988 which, in addition to avoiding disturbance of the penguins, enable assessments of interannual variability in the breeding biology at these colonies.

2.2 Methods

2.2.1 Location of the colonies

The location and terrain of the colony sites are discussed in Chapter 1, Figure 1.2. While at the colony, Auster penguins had several kilometres of open sea ice to move around on, whereas the valley occupied by Taylor Glacier penguins restricted them to an area 200 m long and 100 m wide.

2.2.2 Population estimates

Emperor penguin populations are most easily counted at breeding colonies in mid-winter, when males remain at the colony to incubate the eggs and females are at sea foraging (Robertson 1992). At this time therefore, each male present on land represents a breeding pair. In this study, mid-winter counts of the birds were obtained from composite photographs taken at Taylor Glacier on 26 June, from a 30 m high ridge beside the colony and at Auster on 15 July, with a remotely-triggered camera suspended beneath a helium-filled balloon and directed over the colony at an altitude of 100–200 m (see Table 2.1).

Table 2.1 *Summary of the techniques employed to count emperor penguin adults in mid-winter and pre-fledging chicks in summer at the Auster and Taylor Glacier colonies.*

	Auster				**Taylor Glacier**	
	Mid-winter		Summer		Mid-winter	Summer
		Ground	Tower	Aerial		
Date	15-Jul	1-Dec	1-Dec	10-Dec	25-Jun	26-Nov
Angle	Vertical	Side-on	Side-on	Oblique	Oblique	Oblique
Lens	35 mm	*	*	200 mm	200 mm	200 mm
Format	bl. & white	*	*	colour	colour	colour
Altitude	100-200 m	0	3m	1000 m	30m	30 m

* These observations were taken by eye.

A potential error in employing the mid-winter counts as predictors of breeding pairs is that, in addition to the incubating males, the colonies also contain non-breeders or failed breeders which Prévost (1961) termed 'unemployed birds'. These birds perhaps remain at the colony to practice incubating procedures for future breeding attempts. The proportion of unemployed birds present may vary between locations and between years and needs to be accounted for in breeding pair estimates.

A more accurate, but more difficult to obtain, estimate of the number of breeding pairs at an emperor penguin colony comes from summing the number of pre-fledging chicks in early summer, and the number of failed eggs and chicks during the year. Failed eggs and chicks are covered quickly by drifting snow and require frequent collecting before they become obscured. During this study, it was possible to collect dead eggs and chicks only at the Auster colony, where they were gathered on a near-daily basis between 25 May and 1 December. Pre-fledging chick numbers at Auster were estimated using three separate techniques: a) ground-based counts on 1 December, b) elevated (3 m tower) count on 1 December, and c) count from aerial photographs, taken from a helicopter at 300 m elevation, on 14 December (Table 2.1).

At Taylor Glacier, where it was not possible to count abandoned eggs and dead chicks throughout the breeding period, breeding pairs were estimated using two methods. First, breeding pairs were estimated from males present in mid-winter, assuming the proportion of breeding males to unemployed birds at Taylor Glacier was comparable to that at Auster. The number of unemployed birds at Auster in mid-winter was estimated by subtracting the number of breeding males present, based on the egg and chick counts, from the total number of birds counted. In the second method, I counted live chicks at Taylor Glacier on 26 November (Table 2.1), and added to the live count a predicted number of mortalities to this time, based on the failure rates at Auster.

2.3 Results

2.3.1 Mid-winter counts of birds present

A total of 2 704 ± 14 birds (n = 6 counts) were present in the Taylor Glacier colony on 25 June. At Auster colony on 15 July, approximately 14 760 birds were present. To give the actual standard deviation of the Auster count would confer a false impression of its accuracy. Low light levels and movement of the camera suspended below the balloon caused blurring in the photographs, which reduced the accuracy of counts obtained from them. The error of this count was estimated to be ± 500 birds.

2.3.2 Failures of eggs and chicks at Auster

When Auster penguins huddled tightly (pre-September), only abandoned eggs and dead chicks >50 m from the huddle perimeter were collected; to approach closer than this would have unduly disturbed the brooding parents. The delayed collection meant abandoned eggs and chicks were often recorded several days after their abandonment. It also meant that more abandoned eggs and dead chicks were collected on days the colony moved than on days when it was stationary. After most chicks had been emancipated (after September), and warmer weather induced the birds to huddle less frequently, virtually all the dead chicks present each day could be collected without disturbing the other

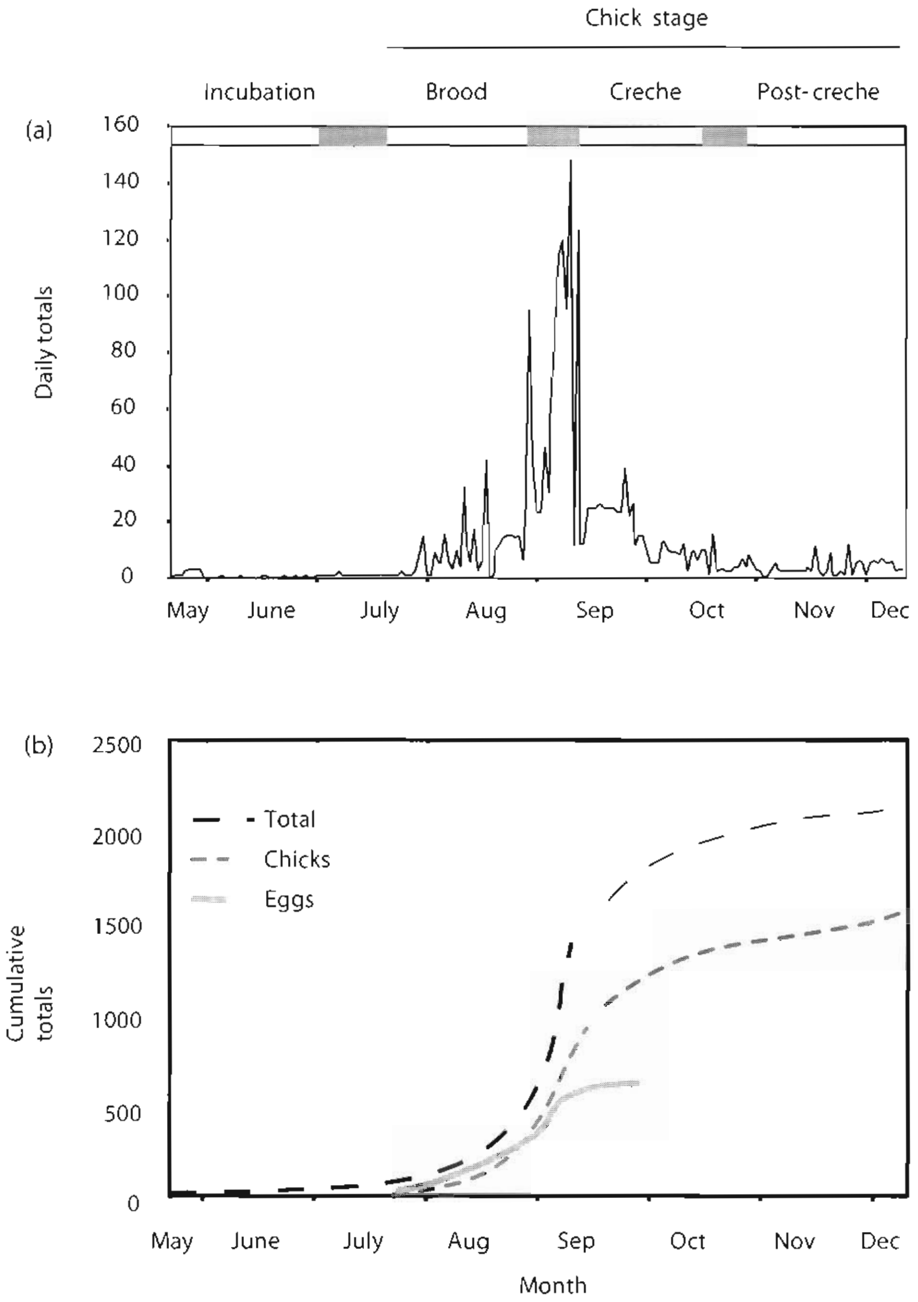


Figure 2.1 *Results from near-daily collections of abandoned eggs and dead chicks at the Auster Colony during 1993; (a) daily totals of eggs and chicks combined, (b) cumulative totals.*

birds.

Failure rates of eggs and chicks at Auster followed a sigmoidal curve after the first abandoned eggs (three) were collected when the colony was first visited on 24 May (Figure 2.1). The number of abandoned eggs was tallied each month and increased from 10 in May to 297 in September, by which time a total of 601 abandoned eggs had been collected (Table 2.2). After September, no more abandoned eggs were sighted. Chicks were first heard calling at the colony on 9 July and the first dead chicks (five) were collected 14 days later, on 23 July. Mortality rates increased through August and peaked on 7 September when 127 chicks died in a single night. After September, the chick mortality rates declined and throughout November just 52 chicks died. In total, 1 543 chicks died and combined with egg failures, 2 144 breeding pairs had failed by 7 December.

***Table 2.2** Monthly egg and chick failures during 1993 at the Auster colony (cumulative totals in brackets).*

Month	Eggs		Chicks		Total	
May	10	(10)	0	(0)	10	(10)
June	15	(25)	0	(0)	15	(25)
July	60	(75)	19	(19)	79	(94)
August	244	(304)	314	(333)	558	(637)
September	297	(601)	887	(1220)	1184	(1821)
October	0	(601)	189	(1409)	189	(2010)
November	0	(601)	52	(1519)	52	(2120)
[a]Dec. 7	0	(601)	24	(1543)	24	(2144)

[a] Field work ended on 7 December.

A source of error in the count of chicks that died was the premature departure of chicks from the colony. During the brooding period, some parents could not wait for their partners to return from foraging trips and headed sea-ward with their chicks on their feet, stopping regularly to ensure the chick was safe. This behaviour was first seen on 22 August and during the following weeks about 10 chicks were seen departing the colony on their parents' feet. After chicks were emancipated, persistent chicks occasionally followed their parents out to sea and presumably died somewhere along the way. About 20 chicks were seen doing this during the early chick crèche period. Based on the amount of time spent observing and the number of small chicks observed departing the colony, it is estimated that approximately 50 chicks died by prematurely departing the colony with their parents and presumably being abandoned somewhere between the colony and the ice-edge. This total was divided amongst the days when this behaviour was sighted and added to the number of known mortalities at the colony.

2.3.3 Pre-fledging chick counts

Of the three techniques employed to count pre-fledging chicks at Auster, the most accurate was the aerial photography. Chicks tended to be concealed behind

Table 2.3*. Pre-fledging chick counts at Auster Colony which had separated into 'suburbs' in 1993. Ground and elevated counts were conducted on 1 December, and aerial oblique photographs were taken on 10 December.*

Suburb	Counting method										
	Ground counts					Elevated 3m	Aerial oblique photographs				
	Person A	Person B	Person C	Mean	+SD	Person A	1	2	3	mean	+SD
Bridgewater	1406	1350	1181	1312	117	1502	2031	2056	2012	2033	22
Glebe	268	250	270	263	11	296	307	303	303	304	2
Hobart	1237	1750	930	1306	414	1562	2217	2222	2209	2216	7
North Auster	1292	2075	1128	1498	506	1491	961	958	954	958	4
NW Auster	(not distinct from West Auster on 1 December)						903	892	888	894	8
West Auster	1613	1590	1339	1514	152	1781	830	832	833	832	2
SB/Taroona	1102	1170	1029	1100	71	1050	1247	1258	1257	1254	6
Blackman's Bay	1310	1550	1301	1387	141	1737	2671	2664	2660	2665	6
Total	8228	9735	6248	8380	700	9419	11,167	11,185	11,116	11,156	26

other chicks when viewed side-on which reduced the accuracy of both the ground and tower-based counts. A total of 11 156 ± 26 chicks were counted (n = 3 replicate counts) from oblique, aerial photographs (Table 2.3). Counts from the 3 m tower recorded 9 419 chicks, 16% fewer than were seen in the aerial photographs, and 8 380 ± 700 chicks were sighted in the ground counts, 25% fewer than the aerial counts (Table 2.3).

At Taylor Glacier, counts of chicks in photographs taken from the 30 m high ridge beside the colony on 26 November, revealed 2 015 pre-fledging chicks, this same total being derived from three separate counts.

2.3.4 Breeding pairs and breeding success

At Auster in 1993, approximately 13 300 eggs were laid (11 156 pre-fledging chicks plus 2 144 accumulated failures), and breeding success to early December was 84% (Table 2.4). In mid-winter at Auster, breeding males comprised approximately 90% of the birds present (13 300 of 14 760 birds) the remaining 10% (1 460 birds) being unemployed male and female birds. At Taylor Glacier, the estimated number of breeding pairs was 2 430, assuming 90% of birds present in winter were breeding males, (90% of 2 704 birds present; Table 2.4). By comparison, assuming breeding success of 84% as at Auster, Taylor Glacier supported approximately 2 400 breeding pairs (1.19 x 2 015 chicks).

Table 2.4 *Summary of population parameters measured at Auster and Taylor Glacier in 1993.*

Parameter measured	Colony	
	Auster	Taylor Glacier
Birds in mid-winter	14 760	2 704
Proportion that were breeding males	90%	
Eggs abandoned	601	
Chick mortalities	1 543	
Chicks live in early summer	11156	2 015
Breeding pairs	13 300	[a]2 400
Breeding success	84%	

[a]estimated

2.4 Discussion

2.4.1 Accuracy of the counts

At Auster colony, the accuracy of the count of birds present in mid-winter was compromised by poor balloon flying conditions. In a two-month period suitably low wind speeds were experienced only twice during a twilight period (the sun remains below the horizon at these latitudes in mid-winter so twilight is he most suitable light ever available), and on only one of these occasions was the sky suitably overcast. (An overcast sky is required because against a clear sky the birds can observe, and are disturbed by, the white balloon).

There appear to be substantial errors associated with ground-based counts of chick numbers at a colony the size of Auster (>10 000 chicks). Oblique, aerial photographs provided a greater accuracy than the ground counts because the birds obscure each other less when seen from a more elevated position. However, using aircraft had the potential to unduly harass the birds. In this study, birds moved away from the 'Squirrel' helicopter which flew at an altitude of 300 m, and this should be considered a minimum over-flight altitude for this aircraft.

The combination of egg and chick mortalities, and counts from aerial photographs of pre-fledging chicks, enabled an accurate estimate of the numbers of breeding pairs, breeding success and mortality rates at Auster. At Taylor Glacier, breeding success and mortality rates could not be measured, and the estimate of breeding pairs relied on an assumption that either the ratio of males to unemployed birds in mid-winter or the breeding success at the colony was comparable to the respective values at Auster. Both the ratio of males to unemployed birds and breeding success probably vary between years and colonies (see below); but as the separate assumptions resulted in similar estimates of breeding pairs at Taylor Glacier, the 2 400 figure probably provides a reasonable approximation of the number of breeding pairs.

2.4.2 Population counts

At Auster in 1993, the number of breeding pairs, chicks raised to pre-fledging age and breeding success (about 13 300, 11 160 and 84%, respectively) were higher than the comparable figures measured at the colony in 1988 (about 10 900 breeding pairs, 8 420 chicks raised and a 77% success rate; Robertson 1992). At Taylor Glacier, there were fewer birds present in the 1993 mid-winter (about 2 700) than in the 1988 mid-winter (about 3 215; Robertson 1992), probably indicating comparatively fewer birds attempted to breed in 1993. In both years, however, approximately the same number of chicks were raised to pre-fledging age (about 2 015 in 1993 and 2 028 in 1988), implying higher breeding success in 1993. These comparisons suggest the foraging environment and/or conditions at the colonies during 1993 were better than in 1988. The data also attest to spatial and interannual variability in conditions experienced by emperor penguins at adjacent colonies on the Mawson Coast, suggesting there are differences in foraging regimes or local weather conditions between the two sites.

Emperor penguins may exhibit a high degree of interannual variability in breeding success. At Pointe Géologie colony, between 1952 and 1987, annual breeding success fluctuated between 5–84% (n = 29 years, mean 61% ± 17.4%; Prévost 1958, Thomas 1986, Jouventin and Weimerskirch 1991). On the Mawson Coast, both the 1988 and 1993 breeding seasons (Robertson 1992, and the present study) may have been better than average years for the emperor penguins, as breeding success in these years was similar to the highest rates recorded at the more frequently studied Pointe Géologie colony.

Population counts at Auster and Taylor Glacier during the 1950s and 1960s suggested the colonies were stable, supporting about 12 000 and 3 000 breeding pairs, respectively (Willing 1958 Budd 1962). Considering inaccuracies of the estimates and the probable interannual variability of breeding numbers (Stonehouse 1964, Thomas 1986, Jouventin and Weimerskirch 1990), these colonies appear to have remained fairly stable since the 1950s. This stability contrasts with the decline, during the same time period, of a colony at Pointe Géologie, which may be attributed to local differences in foraging environments (Jouventin and Weimerskirch 1990, 1991), or investigator-induced changes at the Pointe Géologie colony. The limited counts from other emperor penguin colonies suggest the number of pairs that attempt breeding and/or breeding success may fluctuate (Stonehouse 1964, Budd 1962, Kooyman 1993), but the counts are insufficient to demonstrate any overall trends.

The percentage of unemployed birds present at Auster in mid-winter 1993 (about 10%) was comparable with estimates of this percentage at Auster in previous years (12% in 1988, Robertson 1992, and 10%, range 4–16%, n = 12 counts at Auster and other Mawson Coast colonies in the 1950's, Budd 1962). At Pointe Géologie in the early 1950's, the percentage of unemployed birds in winter was also 10% (Prévost 1953), and this proportion may be relatively constant for emperor penguin colonies. By subtracting this percentage from winter counts of birds present, a reasonably accurate estimate of the number of breeding pairs at an emperor penguin colony may be provided. However, a more accurate estimate of breeding numbers could be provided from counts of egg and chick failures throughout the year, plus chicks surviving in early summer.

2.4.3 Egg and chick failures

A number of factors influence egg and chick failures at emperor penguin colonies. At Pointe Géologie, for example, accidental damage to, or exposure of eggs and brooded chicks were identified as regular causes of failure, as were egg infertility and chick malnutrition (Prévost 1958). The exact causes of egg and chick mortality were not determined in the present study; however, it is reasonable to suppose that similar factors influence egg and chick mortalities at Auster and Taylor Glacier colonies as have been identified elsewhere.

Predation played a variable role in egg and chick failures at Pointe Géologie. In one year, southern giant-petrels (*Macronectes giganteus*) arrived at the colony in September and caused up to 35% of the chick mortalities for the year (Prévost 1958). In the present study, no predators were observed at Auster and Taylor Glacier until November when southern giant-petrels and south polar skuas (*Catharacta maccormicki*) arrived. Rather than attacking live or moribund chicks, these predators focused on scavenging dead chicks and penguin faeces. It was concluded that, at least in 1993, predators on land were not a major factor influencing chick mortality at these two Mawson Coast colonies.

Abiotic factors can also contribute to egg and chick failures at emperor penguin colonies. At Auster, for example, several times during the incubation period, accumulations of fresh snow forced the sea ice down to below sea level, causing an up-welling of seawater and the appearance of pools of slushy snow around the colony. Twice incubating penguins were observed to walk through these slush pools with eggs on their feet and this presumably cooled the eggs potentially to the point of killing the embryos.

On occasions, abiotic factors influence breeding failure in a more catastrophic manner. At Auster in 1968, for example, a rolling iceberg killed many chicks (Cameron 1969), and in 1985, rafting sea ice resulted in many mortalities (Anon. 1985). The tendency for many emperor penguin colonies to be situated near icebergs or ice-cliffs makes them susceptible to catastrophic events (Todd 1980).

During 1993 at Auster, September appeared to be a critical time of the breeding season. During September, which coincided with the period of chick emancipation, 55% of the failures for the entire breeding period occurred. September was also recognised as a critical time for emperor chicks at the Pointe Géologie colony (Jouventin 1975). The chicks that succumbed during the emancipation period possibly had inadequate insulation and fat reserves to survive the extreme cold (< –20°C) and prolonged fasts experienced once they were released by their parents.

Interannual variation in egg and chick failure was evident at both Auster and Taylor Glacier. More abandoned eggs and fewer dead chicks were collected at Auster in 1993 (601 and 1 543 respectively) than in 1988 (397 eggs and 21 54 chicks; Robertson 1992) despite comparable collection efforts between the years. Without a detailed assessment of age and breeding experience each year, as well as the effects of sea ice cover, prey abundance, and the timing and ferocity of inclement weather, it is difficult to pose explanations for the interannual variation in mortality described here. The 32% higher egg failure in 1993 compared with 1988, however, may have been influenced by the occurrence of slushy snow during the incubation phase leading to embryo deaths. Slushy snow was not observed in 1988, which was a year of low snow accumulation (Graham Robertson pers. comm.). By contrast, there were 23% fewer failures overall at Auster in 1993 than in 1988 (2 079 and 2 551 respectively, by 21 November), suggesting that overall conditions were better for chick rearing during the later season.

2.4.4 Emperor penguin colony locations

The location of the Auster colony on sea ice 15 km from the coast provided several advantages for the Auster penguins that were not experienced by penguins at Taylor Glacier. Firstly, the katabatic winds along the Mawson Coast are strongest on the coast, but quickly abate offshore, which means Auster penguins had less exposure to strong winds than Taylor Glacier penguins. Secondly, the large area of sea ice occupied by the Auster penguins provided them with more fresh snow to eat than was available to peguins at Taylor Glacier, where the strong winds and a confined area limited snow availability. Both chicks and adults often eat fresh snow (pers. obs.), probably to reduce dehydration during long periods of fasting (Groscolas 1990). Birds at Taylor Glacier therefore may be more prone to dehydration than Auster birds. A third advantage for the Auster penguins was that their chicks remained clean and dry all year. They would need less enegy to maintain normal body temperature than the chicks at Taylor Glacier, which became wet and dirty on warm spring days when the ice-surface became covered with dirty melt-pools.

The apparent restrictive conditions at Taylor Glacier may have influenced the colony's small population size, compared to Auster colony, although the different foraging environments are also likely to be important in determining population size. However, Taylor Glacier does have one advantage over Auster, it is situated on land, so has the advantage that if sea ice breaks out early, the chicks remain safe.

Both Auster and Taylor Glacier are further from open water than most other emperor penguin colonies (Budd 1961, Kooyman 1993). Adults from Auster and Taylor Glacier must cross at least 50 km of fast ice to reach open water, whereas in the Ross Sea area of Antarctica, emperor penguin colonies are rarely >10 km from open water (Kooyman and Mullins 1990). Despite their distance from foraging grounds, penguins at Auster and Taylor Glacier obviously survive and breed successfully. There are many emperor penguin colonies that are smaller in size than Taylor Glacier, and only a few that are bigger than Auster, although two colonies in the Ross Sea each support 25–30 000 breeding pairs (Kooyman et al. 1990, Kooyman 1993). Further information is required on the foraging regimes of penguins at different locations to better understand the factors influencing colony size.

3. THE ENERGY ASSIMILATION EFFICIENCY OF EMPEROR PENGUINS FED A DIET OF ANTARCTIC KRILL

3.1 Introduction

In most places where penguins occur, they are major consumers of marine resources and in Antarctica, the most abundant food resource is Antarctic krill (*Euphausia superba*; Croxall et al. 1984). Accurate estimates of the quantities of krill consumed by penguins are important to the management and conservation of the Antarctic marine environment and, when based on the energy requirements of the penguins, require both quantitative studies of dietary composition and knowledge of assimilation efficiencies. To date, however, there have been few assessments of the krill assimilation efficiencies of penguins. Such research involves experimentation on captive individuals, which is difficult in the Antarctic environment. In this chapter, I determine the emperor penguin's (*Aptenodytes forsteri*) energy assimilation efficiency when fed a diet of krill, which can constitute over 50% of the penguins' diet at some locations (Klages 1989; see Chapters 4 and 5). This study complements a prior assessment of the emperor penguins' ability to assimilate energy from fish and squid (Robertson and Newgrain 1992) and represents the first study of krill assimilation efficiency by healthy adult penguins.

This study had two additional aims. One was to test the accuracy of the dilution of tritiated water (tritium) as an estimator of krill consumption rates by emperor penguins. Tritium-based estimates of body water turnover are often employed to predict energetic requirements and food consumption by penguins (review in Green and Gales 1990) though their accuracy has rarely been experimentally tested. A further aim was to determine if the period of captivity of penguins for isotope equilibration could be reduced. Periods of up to 4 hours in captivity (Gales 1989) may cause the birds undue stress. I assessed rates of tritium equilibration in the penguins' bodies during the first few hours following injection to see if a reduction in containment time could be achieved without compromising the accuracy of body water estimates.

3.2 Methods

3.2.1 Energy Assimilation Efficiency

I assessed the krill assimilation efficiency of nonbreeding emperor penguins from the Auster colony (67°23'S; 64°04'E), Mawson Coast, Antarctica, in June 1993. Three penguins were selected at random, weighed, and taken to a field camp 8 km from the colony. Three additional penguins of a size similar to the experimental birds were caught and their stomachs flushed to verify that the nonbreeding birds were fasting. Their stomachs contained stones, heavily digested squid beaks, and bile, which indicated that they had not fed recently.

The penguins were housed individually in pens (1.5 m^2, padded and plastic lined) erected in a field hut. The hut kept out wind and snow and maintained ambient temperatures of –15 to –30°C. Each pen had a floor of 1.5 cm wire-mesh through which the penguins' excrement (urine and faeces) passed into collecting trays. The penguins were held in the pens for 24 hours, reweighed, and then injected in the pectoral muscle with tritiated water (10 mCi in 1.0 mL distilled water). Blood samples (2 mL) were taken from each penguin's radial vein at intervals during the isotope's equilibration and turnover periods as described below. Twenty-four hours after injection, the collecting trays below the pens were scraped clean, and the penguins were force-fed 1 kg of homogenised krill. The krill had been trawled from waters off the Mawson Coast in February 1993, packaged in 1 kg lots, snap frozen in a blast freezer, and stored until required. At feeding, packets of krill were defrosted carefully (to avoid moisture loss), homogenised, weighed (± 1 g), and ejected from a pastry bag through a plastic tube (40 cm long, 2 cm outer diameter) into the penguins' stomachs. Any unconsumed krill was weighed and subtracted from the original weight to record the exact amount ingested by each penguin.

Two of the three penguins swallowed 1.0 –1.5 kg of krill daily for 11 days, the third penguin vomited on the second day; a fourth penguin that replaced it consumed 8.5 kg in 6 days before logistic constraints ended the experiment. On its release, the third penguin promptly ate snow, which suggests that it became dehydrated during the experiment. Thereafter, up to 100 mL of melted glacier ice was added to the krill homogenate fed to each experimental bird. In total, the added water constituted < 5% of the penguins' water intake. Twenty-four hours after their final feeding, a blood sample was drawn from each penguin. The penguins were then weighed, their stomachs were flushed to determine the amount of food that was undigested, and they were returned to Auster colony.

The penguins' stomach contents (drained of excess water through a 0.5 mm sieve) and excrement (collected separately after 6 and 11 days) were frozen and stored along with daily samples of the homogenised krill. In the laboratory, the weights of subsamples from the krill, stomach contents and excrement were recorded after oven drying (60°C) to constant mass. To determine their energy content, duplicate samples were pulverised, compressed into pellets, weighed and combusted in a ballistic bomb calorimeter. The penguins' energy assimilation efficiency was calculated as the difference between gross energy intake and gross energy output (Kendeigh 1949).

3.2.2 Isotope Equilibration Rates

The time required for tritium to equilibrate with the penguins' body water was investigated for the four penguins in the assimilation efficiency experiment and a further five randomly selected, nonbreeding birds from the Auster colony. Following the injection of tritium, blood samples were drawn from three penguins from the assimilation efficiency experiment after 1.0 and 2.0 hours, and from the fourth penguin after 0.5, 1.5, and 2.0 h. The second group of birds was caught later in the year (October) , when time was available between other studies. Five cage pens (each 4 m^2) were erected on the sea ice adjacent to the Auster colony to house the penguins, which were weighed and injected as before. Blood samples were drawn from these birds at intervals of 0.5, 1.5, 2, 2.5, and 3.5 hours following the injections.

3.2.3 Water Turnover Calculations

Blood samples were stored frozen and returned to the laboratory, where water was extracted from them by vacuum distillation (Vaughan and Boling 1961). Aliquots of 10 µL of this water were added to 10 mL of scintillation cocktail (Optiphase-Hisafe, Wallac Scintillation Products, Turku) and assayed for tritium activity, to 1.0% accuracy, in a liquid scintillation counter (Rackbeta 2, Wallac Scintillation Products, Turku). Initial body water pool sizes were determined by comparing blood isotope levels 2 hours after injection with standard solutions containing 10 µL of tritium isotope in distilled water (1:5000).

The water turnover rates were estimated (with equation 4 in Nagy and Costa 1980) after 6 days (one bird) and 11 days (two birds) of feeding, when krill consumption amounted to approximately 40% and 60%, respectively, of the penguins' original body mass.

Dietary water intake was determined by combining measurements of free water (mass change through oven drying at 60°C) and estimates of metabolic water based on average amounts of lipid and protein in the diet. Dietary lipids were determined by lipid extraction (for 18 hours), with carbon tetrachloride as the solvent in a Soxhlet apparatus. Subsamples were then ashed in a muffle furnace at 550°C and the protein mass was assumed to equal the mass of the dry matter minus the masses of the ash and lipid fractions. The oxidation of lipid and protein yields 1.07 mL/g and 0.5 mL/g of water, respectively (Schmidt-Nielsen 1975). The actual water intake was compared with isotopically-derived water intake to assess the accuracy of the tritium technique.

3.3 Results

3.3.1 Energy Assimilation Efficiency

The dry mass energy content of the homogenised krill averaged 21.35 ± 1.30 kJ/g (n = 10 samples). The dry weight of the residual food in the penguins' stomachs was 35.55 ± 15.37 g and as it had lost none of its energy value (22.20 ± 0.97 kJ/g, n = 3), the weight of this food was subtracted from the amounts consumed. Table 3.1 shows the penguins' weight change, duration of feeding, food intake, excretory output, dry matter absorption, and energy assimilation efficiency. All three penguins maintained constant masses (0.1% ± 1.2% change) for the duration of the experiment. They absorbed 48.9% ± 2.3% of the dry-matter contained in the krill diet and the energy content of their excrement was 12.32 ± 0.18 kJ/g, with no difference between excrement collected from the first 6 days and the last 5 days of feeding (paired t-test, $t = 0.55$, df = 1, $p = 0.677$). The energy assimilation efficiencies of the three penguins averaged 70.5% ± 1.7%.

3.3.2 Isotope Equilibration Rates

In June, the penguins had significantly lower total body water pools (502 ± 35 mL/kg body mass, n = 4) than those in the October group (626 ± 31 mL/kg body mass, n = 5; paired t-test, $t = 5.63$, df = 7, $p < 0.001$). The estimated pool sizes at intervals during the tritium equilibration were converted to percentages of the 2 hour estimate (Figure 3.1). Following injection, tritium spread quickly in the free body water. Body water pools predicted from blood samples drawn after

Table 3.1 *Results of an energy assimilation efficiency experiment on three emperors that were hand-fed a diet of Antarctic krill.*

Emperor Penguin no.	Body Mass (kg)	Mass change (%)	Duration (d)	[a]Food intake				Excretory output			Dry Matter Absorbed (%)	Energy Assimilation Efficiency (%)
				Wet mass (kg)	Dry mass (kg)	Energy (kJ/g)	(kJ)	Dry mass (kg)	Energy (kJ/g)	(kJ)		
1	28.2	0	11	16.33	3.521	21.35	75270	1.79	12.20	21840	49.2	71.0
2	32.0	1.3	11	16.11	3.473	21.35	74160	1.86	12.51	23270	46.4	68.6
3	26.5	-1.1	6	8.43	1.818	21.35	38800	0.89	12.19	10850	51.0	72.0
Mean	28.9	0.1							12.30		48.9	70.5
±SD	2.8	1.2							0.18		2.3	1.7

[a] The mass of the undigested material in the penguins' stomach 24 h after the final feed was subtracted from the food intake.

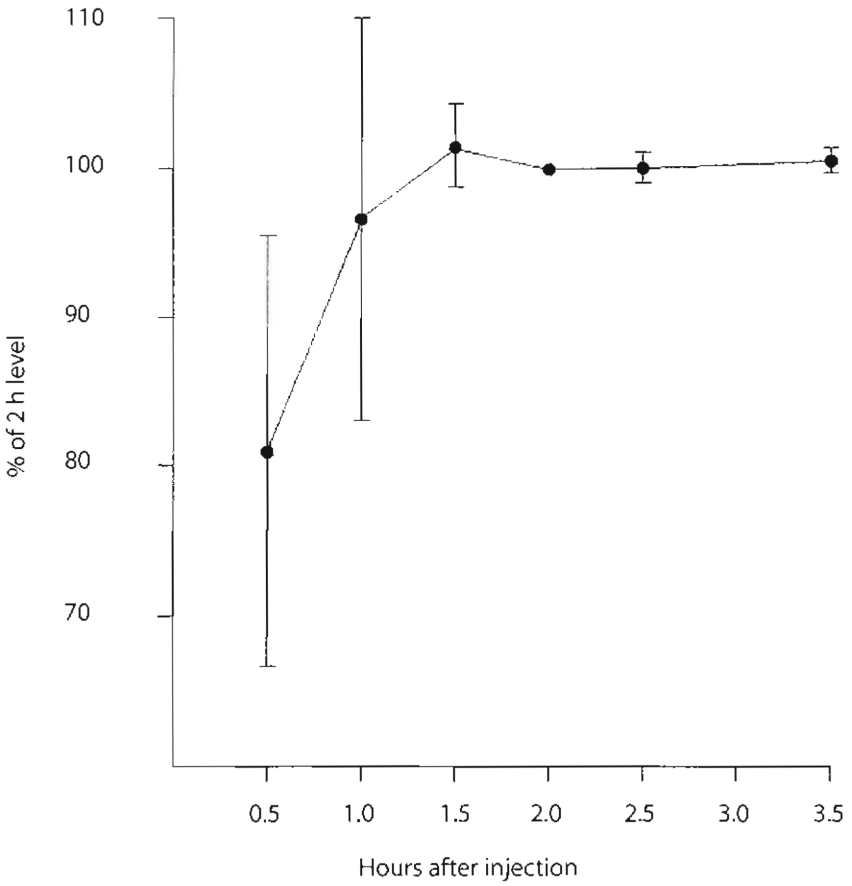


Figure 3.1 *Tritium based estimates of body water content over the first 3.5 h after tritium injection expressed as a percentage (± 1 SD) of the estimate at 2 h (*n = *3 to 9 penguins for each time).*

3.3.3 Accuracy of the Tritium-Derived Water Intake

In the free body water of the three penguins hand-fed krill, tritium activity reduced by 55.7% ± 13.3% from the equilibration levels. The isotopically -derived estimates of their water intake averaged 44.65 ± 3.06 mL/kg·d^{-1} (n = 3 penguins).

The water content of the homogenised krill diet was 901 ± 8 mL/kg (n = 5 samples), comprising 776 ± 19 mL/kg free water and 125 ± 22 mL/kg metabolic water. Combining the water content of krill with the rate of feeding, the measured rate of water intake by the penguins was 49.35 ± 4.28 mL/(kg/day) which was significantly different to the isotopically-derived estimate (paired t-test, $t = 5.99$, df = 2, $p = 0.013$; Table 3.2). The tritium technique underestimated actual water intake by 9.4% ± 2.4% (Table 3.2).

Table 3.2 *Water intake as estimated by the tritium dilution method and actual water-intake measured gravimetrically for emperor penguins hand-fed Antarctic krill.*

[a]Penguin	Water intake			Error of the tritium method (%)
	Tritium method estimate		[b]Actual daily rate (mL/kg)	
	Change in activity (%)	Daily rate (mL/kg)		
1	63.5	44.10	50.19	-12.1
2	63.1	41.89	45.33	-7.6
3	40.3	47.95	52.34	-8.4
Mean	55.7	44.65	49.29	-9.4
± SD	13.3	3.07	3.59	2.4

[a]Penguin numbers correspond with those in Table 3.1.

[b]Rates are calculated from preformed plus metabolic water in the krill diet.

3.4 Discussion

3.4.1 Energy Assimilation Efficiency

The estimated assimilation efficiency of krill-fed emperor penguins was 70.5%, which is within the range of values obtained for emperors and other penguin species on a crustacean diet (63.3–82.8%; Table 3.3). This range is quite broad (20% variation in digestive efficiencies) and may reflect adaptive differences in the digestive systems of the penguin species (Jackson 1990). However, all penguins exploit similar prey types, and it seems unlikely that interspecific differences alone can account for the broad range in their krill digestion efficiencies.

Emperor penguins assimilate significantly less energy from krill (this study) than from their other main dietary components, fish and squid (81.8% and 76.2%, respectively; see Robertson and Newgrain 1992, also a study of fasting, nonbreeding emperor penguins; *t*-tests following arcsine √ transformation, $p < 0.005$ in both comparisons). Furthermore, penguins in general appear to digest crustaceans (72.9% ± 6.7%, $n = 6$ studies) slightly less efficiently than other dietary components (fish, 76.6% ± 10.6%, $n = 6$ studies; squid, 75.2% ± 3.9%, $n = 6$ studies; Table 3.3), though the differences were not significant (*t*-test, $p > 0.05$ in all comparisons). The slightly lower efficiency of assimilating krill is unlikely to be related to difficulties in digesting chitin, as the chitin content of krill is low and penguins are efficient at digesting it (Jackson et al. 1992). Comparatively low fat levels and high protein levels can also reduce assimilation efficiency (Castro et al. 1989), but the krill here had a higher lipid content (19.6% of dry mass) and lower protein content (69.2% of dry mass) than krill in other studies (3.5–11.2% lipid and 73–90% protein; Jackson 1990). Culik (1987) found fluoride (which may be toxic in large concentrations) amounts were almost five times higher in krill cuticle fragments excreted by Adélie penguins (*Pygoscelis adeliae*) than in fresh cuticle. Perhaps penguins digest crustaceans with less efficiency than they digest other prey as a metabolic adaptation that reduces fluoride intake.

Although the differences among studies in assimilation efficiencies may reflect dietary or interspecies variations, they also may be influenced by variations in experimental procedures. Sources of error with the present study may be that the penguins had been fasting and may not have been physiologically prepared to digest a meal, and that they were fed krill that had been homogenised. If, for exogenous reasons, the force-fed birds were not storing energy or nutrients, then the food might not have been completely digested, in which case the assimilation efficiency would be underestimated (Castro et al. 1989). However, excrement collected separately from the first 6 days and the last 5 days of the penguin feeding had the same energy value (both 12.3 kJ/g), which suggests that the assimilation efficiencies of the penguins were constant for the two periods and that the onset of digestion by these fasting birds was not retarded. Also, the daily meal size fed to the birds (1.5 ± 0.3 kg, $n = 28$ meals) was not likely to have overtaxed their digestive systems and reduced their energy assimilation efficiency. For example, the food consumption rates estimated for free-ranging emperor penguins (1.8 to 6.0 kg/d, Robertson 1994, Chapters 4 and 5) greatly exceed the rates that the birds were fed. Although these estimates were for active rather than passive birds, the amounts indicate that emperor penguins are capable of digesting far greater quantities than recorded here. Moreover, it is unlikely that the birds would eliminate potential nutrients and energy when being fed a standard dietary item at rates that approximate normal daily consumption rates.

Table 3.3 *Energy assimilation efficiencies for penguins hand-fed various dietary items. Healthy adults were studied, except by Cooper (1977; chicks), Copestake et al. (1983; a starved bird regaining its strength) and Davis et al. (1989; two fledglings).*

Diet	Penguin species	Duration		Mass Change	Assimilation efficiency (%)		Source
		(n)	(d)	(%)	Mean	± SD	
fish	emperor	2	12	1.2	81.8	0.9	Robertson and Newgrain 1992
	king	1	7,4[a]	14.3	94.2		Copestake et al. 1983
	king	6	2-4	-2.5	68.8	11.0	Jackson 1990
	gentoo	6	2-4	-1.2	79.1	4.6	Jackson 1990
	rockhopper	6	2-4	-3.2	65.5	5.2	Jackson 1990
	jackass	4	16-50	+	76.5	2.2	Cooper 1977
	little	3	5	-2.0	70.5	0.8	Gales 1989
squid	emperor	4	3-7	3.2	76.2	1.2	Robertson and Newgrain 1992
	king	4	5	n.r.	81.3	n.r.	Adams 1984
	king	5	2-4	- 0.6	76.3	1.7	Jackson 1990
	rockhopper	6	2-4	-3.9	74.9	5.2	Jackson 1990
	gentoo	6	2-4	-1.9	69.5	4.4	Jackson 1990
	little	3	5	-1.0	73.0	1.5	Gales 1989
crustacean	emperor	3	6-11	0	70.5	1.7	Present study[b]
	king	1	4	12.0	82.8		Copestake et al. 1983[b]
	king	2	2-4	-2.9	63.3		Jackson 1990
	rockhopper	5	2-4	-4.0	70.0	5.2	Jackson 1990
	gentoo	3	2-4	-3.3	77.4	8.9	Jackson 1990
	gentoo	2	7	n.r.	73.5	3.5	Davis et al. 1989[b]

[a] Two determinations were made for the same penguin.

[b] Penguins fed Antarctic krill, *Euphausia superba*.

The krill fed to penguins were homogenised to facilitate their injection into the penguins' stomachs. Having been frozen and thawed, the krill already had been mashed to some extent, and to feed them individually to the penguins would have been messy, slow and more stressful for the penguins. Previously, to obtain assimilation efficiencies for penguins, krill have been homogenised (Davis et al. 1989), encased in an agar jelly (Copestake et al. 1983) or substituted by a prawn (*Penaeus indicus*; Jackson 1990). Thus, all studies of krill assimilation by penguins have involved modifying the diet and this may have influenced the generally lower assimilation efficiencies recorded for this prey.

Errors that may have influenced results in other studies on penguins but were accounted for in the present study were weight loss and unquantified food in the penguins' stomachs. Penguins in the present study maintained constant body masses, while in previous studies, weight losses of 4% have been recorded (see Table 3.3). Assimilation efficiency can be underestimated in birds that lose mass (Blem 1976). Also, in the present study, 160 ± 90 g of undigested krill flushed from the penguins at the end of the experiment reduced the recorded digestive efficiency by only 0.4%. The amount of food undigested would be further increased if the penguins were fed large prey items that could be digested more slowly than the homogenised diet fed in this study. The retention time of food in the stomach of seabirds varies according to diet and seabird species (Jackson 1990) and should be accounted for in all assimilation efficiency studies.

3.4.2 Isotope equilibration rates

Isotope equilibration rates vary with injection technique, metabolic rate, and mass of the animal (Nagy and Costa 1980). In emperor penguins, Robertson and Newgrain (1992) found that tritium had equilibrated with body water pools within 2 hours of intramuscular injection and remained at constant levels for at least 24 hours. The present study found that tritium levels in the blood could approach equilibration just 30 min post-injection in some individuals but did not achieve equilibration in all individuals until after 1.5 h. Tritium levels in the blood did not alter significantly up to 3.5 hours post-injection. For consistent estimates of body water pool sizes, blood samples should be drawn from emperor penguins 1.5–3.5 hours post-injection. A shortening of the 2.0 hour injection-to-bleed time, recommended by Robertson and Newgrain (1992), to 1.5 hours represents a 25% reduction in the time a bird needs to be held captive, and a reduction in the birds' stress could be expected.

3.4.3 Accuracy of isotope-derived water intake

The tritium method underestimated actual water intake of emperor penguins fed a krill diet by 9.4% ± 2.4%. Previously, the tritium method has underestimated water intake by emperor penguins on diets of squid and fish by 9.4% ± 1.1% and 1.1% ± 8.6% respectively (Robertson and Newgrain 1992). Diet type does not influence the accuracy of the tritium technique (t-tests following arcsine $\sqrt{}$ transformation, $p > 0.05$ for all comparisons), though differences could be masked by individual variations between penguins and by the small sample sizes used in experiments. Overall, water intake estimated by tritium turnover for emperor penguins consuming their three main diet components is 6.87% ± 6.54% ($n = 11$ penguins) less than actual water intake.

In contrast to the finding for emperor penguins, tritium turnover overestimated water intake in little penguins (*Eudyptula minor*) by 6.50% ± 7.84% (estimated from Gales 1989). The different humidities in which the experiments were conducted may have influenced the results. At higher humidities, moisture taken in across respiratory surfaces may dilute the tritium causing higher water turnover estimates, while at lower humidities, greater moisture loss and the preferential loss of the lighter, unlabelled water molecules concentrates the tritium causing lower water turnover estimates (Nagy and Costa 1980). The study of little penguins was conducted in Tasmania, in an absolute humidity of approximately 7.25 g/kg, while studies on emperor penguins were conducted in Antarctica, at absolute humidities of around 0.40 g/kg (calculated from data provided by Bureau of Meteorology, Hobart). Perhaps tritium was concentrated to a greater extent in the emperor penguins in the drier Antarctic than in the little penguins in Tasmania.

In conclusion, the use of the tritium method to estimate water intake by captive emperor penguins fed their three main prey types underestimates water turnover by around 7%. This error is similar to that reported for a range of other animals (summaries in Nagy and Costa 1980, Degen et al. 1981). However, if the size and direction of this error is known and certain assumptions are met (Nagy and Costa 1980), the tritium technique provides an inexpensive and accurate method for estimating water flux from which energetic requirements of emperor penguins can be estimated.

4. THE FORAGING ECOLOGY OF FEMALE EMPEROR PENGUINS IN WINTER

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4.1 Introduction

In antarctic oceans during winter, the solar influence reaches its lowest level for the year and a blanket of fast ice covers inshore waters for up to 100 km from the coast. This fast ice restricts access to food by air-breathing marine predators, forcing them to forage in polynyas (areas of open water within regions of sea ice) over the continental shelf or off the shelf in pack ice regions. As a result, most antarctic seabird and seal species poduce their young in spring and summer when the weather is mildest and the fast ice breaks up making prey accessible adjacent to coastal breeding sites. Although the foraging ecology of Antarctic species in summer is becoming well known (e.g. Bengtson et al. 1993, Chappell et al. 1993) winter foraging patterns are poorly understood. Considering the marked seasonality in prey availability, winter foraging patterns of Antarctic predators may differ substantially from the summer foraging patterns currently recognised. Winter studies are required to understand better the diversity within Antarctic ecosystems and the resource requirements of the major predators.

Emperor penguins (*Aptenodytes forsteri*) are the largest of all seabirds (up to 40 kg body mass) and their circumpolar distribution and population of an estimated 200 000 breeding pairs (Woehler 1993) make them important predators in the antarctic marine environment. Unlike most antarctic seals and seabirds, which produce their young in spring and summer, emperor penguins court in early autumn, each female laying a single egg in late autumn. The females relinquish their eggs to their partners and leave the colony to forage at sea for two months (Stonehouse 1953, Prévost 1961). When the chicks hatch at the end of winter, the females return to the colony. Because females depart at the start of winter and return at the end of winter, they are ideal subjects on which to deploy and recover instruments that can monitor winter conditions. Such a study could not only reveal the winter foraging patterns of emperor penguins, but could also yield important information on antarctic marine ecosystems in winter.

The foraging strategy of female emperors in winter may have been integral to the evolution of the species' unique breeding strategy. While at sea, the females must catch sufficient prey to rebuild energy stores depleted by their fast before egg-laying and by egg production. They must also accumulate fat to provide the energy for their forthcoming chick-brooding and gather food to nourish the chick in the early stages of its development. While the females are at sea, the male emperors remain at the colony to incubate the eggs in ambient air temperatures ranging from –10°C to –40°C. By the time the females return, the males have fasted for a total of 110–115 days and lost approximately 40% of their body mass (Prévost 1961). Primary egg care by males is unusual in birds (Skutch 1957, Oring 1982); an understanding of what has contributed to this strategy in emperor penguins may help us to understand the evolution of avian breeding strategies in harsh environments. Although adaptations of male emperors to survival during winter are known (Le Maho 1977, Groscolas 1990) we currently lack information concerning the females at this time. An assessment of the females' foraging ecology in winter could help to explain the adoption of a single incubation shift by emperor penguins.

This study provides the first account of the foraging ecology of female emperor penguins during winter. I investigated simultaneously the foraging activities of females from two colonies to gain an understanding of the spatial variation in foraging patterns within a single breeding season. My specific aims were to assess where the females foraged in winter, what foraging patterns they adopted, what prey species they ate, and how much food they consumed. The results are compared with emperor penguin foraging behaviour in spring and summer (Robertson 1994 and references therein, Kooyman and Kooyman 1995). The research also provides insights into trophic relationships in Antarctic waters in winter, and elucidates specific pressures that could have influenced the evolution of the emperor penguin's unusual breeding strategy.

4.2 Methods

4.2.1 General

The study was undertaken between May and August 1993 at the Auster (67°23'S, 64°04'E) and Taylor Glacier (67°28'S, 60°54'E) colonies which lie 150 km apart on the Mawson Coast of Antarctica. In winter, both these colonies are separated from open water by up to 100 km of fast ice (Budd 1961). In 1993, about 13 300 and 2 400 pairs of emperor penguins bred at Auster and Taylor Glacier, respectively (see Chapter 2).

In late May, female penguins were caught upon departure, 1 km seaward of their colony. A light-proof hood was placed over the head of each penguin to reduce stress (Kosiorek and van den Hoff 1994), and the penguin's cloaca was examined to ensure that she had recently laid an egg. The penguins were then weighed to ± 0.1 kg, marked on the chest with 'Nyanzol' dye, and processed further as outlined in the following sections. Upon release the penguins were observed for ≥ 30 min to ensure that they continued their journey to the ice-edge. To monitor the return of marked penguins, a presence was maintained at both colonies between mid-July and late August, by which time most of the females had returned. Thereafter, it was logistically feasible to maintain observations at Auster only.

4.2.2 Determining foraging locations

The foraging locations of three Auster females were determined by tracking satellite packs (PTTs, Model ST 6, Telonics Pty Ltd, USA) that transmitted every fourth day and were attached to the birds as they left their colony for the ice-edge. The PTTs were packaged in streamlined epoxy moulds and were attached by hose-clamps and 'Loctite 401' adhesive to feathers on the lower half of the birds' backs to minimise drag (Culik and Wilson 1991, 1992, Culik et al. 1994). The PTTs had a mass of 450 g, measured 11 x 7 x 2 cm, had a 20 cm trailing antenna, and had a frontal surface area of 14 cm^2 (2.4% of the 590 cm^2 cross-sectional area of an average adult bird). Because of their large size, the PTTs could have reduced a penguin's foraging efficiency, causing weak birds to abandon their breeding effort for the year. To reduce this potential impact, I deliberately selected large, robust-looking penguins to carry the PTTs.

4.2.3 Foraging behaviour

Sampling strategy

In May 1993, 12 female emperor penguins departing Auster (including the three birds with PTTs) and six females leaving Taylor Glacier were fitted with time-depth recorders (TDRs, Mk 5, 3 m depth resolution, 0–750 m depth range, Wildlife Computers, USA) modified to allow attachment with hose clamps to penguin feathers. Each TDR contained either 128 Kb or 256 Kb memory, was 100 g in mass, measured 11 x 4 x 1 cm, and had a frontal surface area of 4 cm^2 (<1% of the cross-sectional area of an average adult bird). In addition, three departing Auster penguins were fitted with time-depth-speed recorders ('Paddles', Platypus Engineering, Tasmania) that contained 64 Kb of memory, weighed 250 g, measured 11 x 4 x 2 cm, and had a frontal surface area of 8 cm^2. Penguins fitted with only TDRs or Paddles were selected at random from the departing females. All devices remained securely attached to the penguins for the duration of the study, with the longest period between deployment and recovery of a device being 5 months.

To collect data over the entire winter foraging period, I programed the units to switch on at staggered intervals and sample until the memories were filled. Once activated, the TDRs sampled every five seconds in order to give sufficient detail about the dives (see dive durations in Kooyman et al. 1971, Robertson 1994). Their depth thresholds (below which a diving event was recorded) were set at 6 m, twice the resolution of the TDRs (as recommended by the manufacturers), and the internal clocks were set at Local Solar Time (UTC plus 4 hours).

Analysis of dive data

On retrieval, the TDRs were downloaded to a PC-computer and processed with Zero-offset-correction software (ZOC, Wildlife Computers, USA). The ZOC software allowed drifts in the TDRs' pressure sensors, that may have caused depth readings to be in error by up to 21 m (generally <9 m), to be accounted for, but incorporated user verifications of what constituted a surface reading. Unfortunately, when ZOC analysis was performed twice on identical dive information to test its accuracy, the number of identified dives to depths of 6–10 m differed. However, dives to <10 m were usually of short duration, contained few depth fluctuations, and were assumed to be non-feeding dives (see below); they were excluded from the analysis of the penguins feeding behaviour.

The zero-corrected files were processed with a dive analysis package (DA, Wildlife Computers) that enabled the differentiation of dive types, based on the dive profiles, durations, and maximum depths, into the following categories.

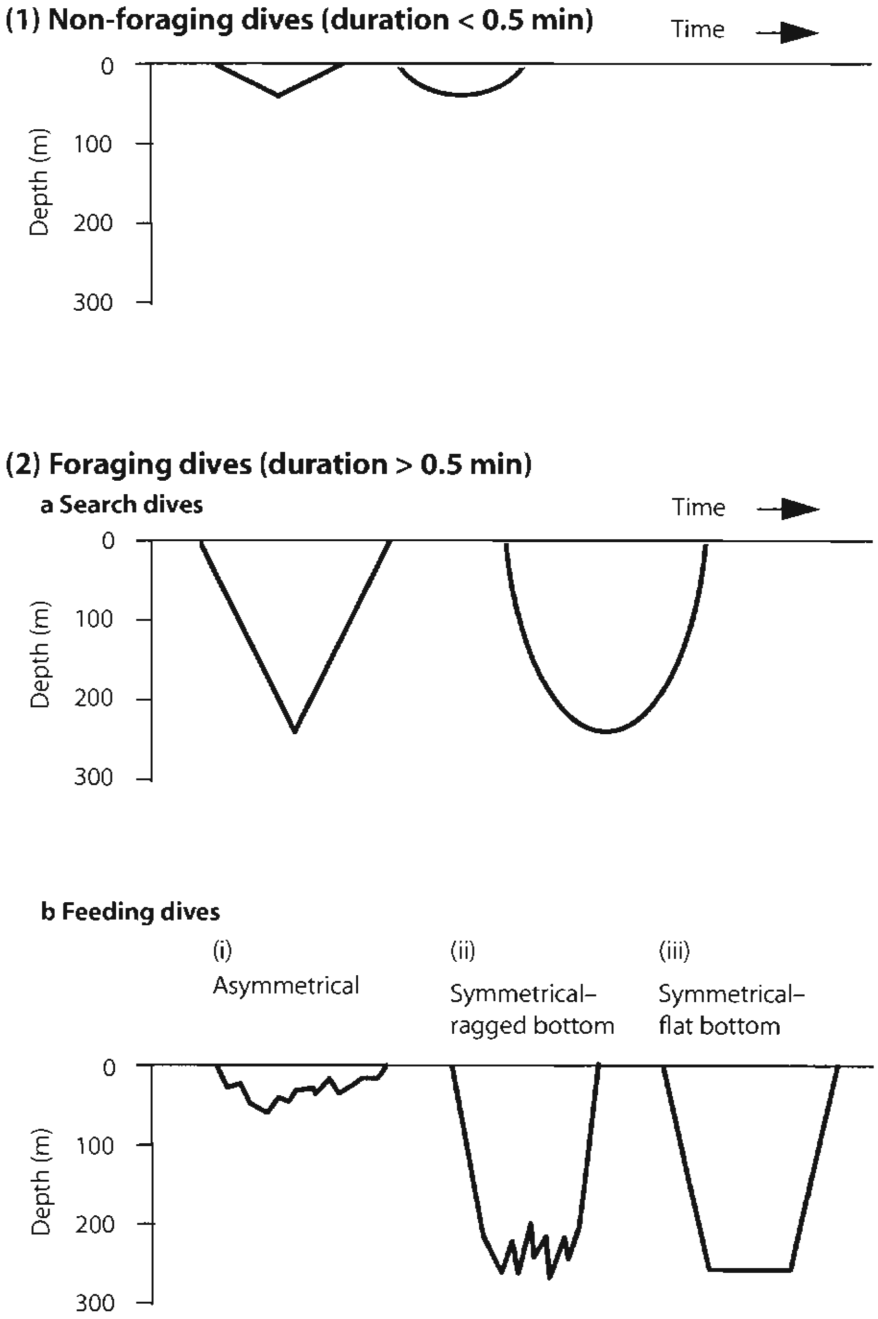

Figure 4.1
Stylised profiles of dive types made by emperor penguins foraging in winter.

1) Non-foraging dives.
The penguins descended and then ascended smoothly in short (2–30 sec duration), shallow (usually 10–20 m, but occasionally to 50 m depth) dives. These dives were either 'V' shaped or 'U' shaped and were often performed in a series of up to 30 dives. I assumed that during these dives the penguins were commuting, recovering from feeding dives, or diving for social or self-maintenance (e.g. grooming) reasons.

2) Foraging dives.
a) Search dives. These dives appeared similar in profile to the non-foraging dives but were longer (0.5–8.0 min duration) and deeper (50–400 m). I assumed penguins performed search dives for navigational or foraging purposes. Because there were no irregularities in the smooth descent/ascent patterns of these dives to indicate prey were caught, I did not include search dives in the analysis of feeding depths.

b) Feeding dives: These were dives to any depth >10 m that contained a distinct descent phase, followed by either a period of depth fluctuations (possibly indicating prey pursuit) or a flat bottom (perhaps indicative of benthic foraging) and an ascent to the surface. I distinguished three types of feeding dives:

i) Asymmetrical feeding dives, usually to depths <100 m, with a distinct descent phase and then a ragged ascent phase.

ii) Symmetrical feeding dives with ragged bottoms, usually to depths >100 m.

iii) Symmetrical feeding dives with flat bottoms, usually to depths >100 m with flat bottoms, assumed to reflect benthic feeding.

Feeding behaviour was assessed from the depth distribution of the penguins' feeding dives, and penguins from the two colonies were compared based on the depths most frequented, dive durations, estimated periods of prey pursuit per dive (bottom time), and depth frequencies of dives containing potential feeding events (wiggles). Bottom time was calculated as the period between the first and last depth reading that was >85% of the maximum depth (the default setting in the DA program). In most symmetrical feeding dives, the calculated bottom time approximated the duration between the points of inflection at the end of descent and the beginning of ascent in the profiles. The bottom time calculation also gave a reasonable approximation of the wiggle time in asymmetrical feeding dives that contained no discrete inflection points in their profiles. Previously (e.g. Kooyman and Kooyman 1995), dives for which inflection points were not discrete were ignored in the analysis of bottom time durations. A wiggle was defined as a depth fluctuation of >6 m (twice the TDRs' resolution) during the bottom time.

4.2.4 Dietary composition

Diet samples were collected from 17 female penguins selected at random as they returned to Auster in late July and early August. The samples were collected using a stomach-flushing technique similar to that of Wilson (1984). Each bird was weighed to ± 0.1 kg and was strapped into a restraining cradle (Robertson

1991). Its stomach was filled gradually with warm (25°C) seawater gravity-fed from a height of 1 m. When the penguin began to regurgitate, it was inverted and its stomach contents were emptied into a bucket. This procedure was repeated until clear water was expelled, usually after 2–3 flushes. Water was drained from the samples (in a 0.5 mm sieve), and the remaining solids were stored frozen for later analysis.

In the laboratory, the stomach samples were defrosted, redrained to similar wetness for all samples, and weighed to ± 0.1 g. Each sample was assessed qualitatively as being heavily, moderately, or lightly digested (after Robertson et al. 1994a) and the dominant prey type (fish, squid or crustacean) was estimated by eye. A 300-g subsample was then taken at random from each sample and Antarctic krill (Euphausia superba) eyes were counted in these subsamples. Each subsample was placed in a plastic dish and irrigated and panned up to 20 times to expose fish otoliths (ear bones), fish jaws, and squid beaks. The number of krill eyes in each subsample divided by two gave an estimate of krill numbers, the number of fish otoliths divided by two gave an estimate of fish numbers and counts of lower beaks plus unpaired upper beaks provided an estimate of the number of squid. The identities of prey were determined with published keys (J Kirkwood 1982 for euphausiids, Williams and McEldowney 1990 for fish, Clarke 1986 for squid) and reference collections held at the Australian Antarctic Division. The size and mass of prey items were predicted from length measurements of non-eroded otoliths, jaws and beaks using published equations (Appendix 4A). Because the body parts of the krill were too digested to measure accurately I assumed the mass of each individual was 0.6 g, which was the mean body mass of krill (excluding gravid females) caught during trawling on the Mawson Coast in January 1993 (Graham Hosie, pers. comm.). A quantitative measure of the diet composition was obtained by combining the masses of the various prey represented in the 300 g subsamples.

4.2.5 Estimating prey consumption rates

The prey consumption rates of the female penguins were estimated by dividing their rates of dietary-water intake (determined by the turnover rate of tritiated water [^3H_2O]) by the water content of the dietary mix. In late May 1993, 25 females departing Auster and six females departing Taylor Glacier (which included all birds carrying devices) were injected in the pectoral muscle with 1.2 mL of distilled water containing 50 mCi (1.85 MBa) of tritium (HTO). The penguins were placed in open pens on the sea ice for 2 hours while the HTO equilibrated with their body-water pools. A 2 mL blood sample was then drawn from the radial vein before the birds' release. I used glass syringes for all HTO injections to ensure accuracy of the volume injected; disposable syringes were used for blood withdrawals. When the penguins were recaught on their return to the colony after winter, a second blood sample was taken. To record background radioactivity levels, I also took blood samples from five returning penguins not injected with HTO. All blood samples were sealed in screw-top 'Cryotubes', wrapped in waxed paper and stored frozen for later analysis.

In the laboratory, water was extracted from the blood samples by vacuum sublimation (Vaughan and Boling 1961). Duplicate 100 µL aliquots of water from each sample were added to vials containing 10 mL of scintillation cocktail, and each was assayed for radioactivity in a liquid scintillation counter. The specific activity of the HTO injected was determined from 10-µL aliquots of dilutions (1:5000) of the field stock solution in distilled water that were added to 10 mL of scintillation cocktail and assayed for radioactivity. Background radioactivity levels recorded in both distilled water 'blanks' (10 µL in 10 mL of scintillation cocktail) and blood samples from nontritiated penguins were similar; the respective values were subtracted from the number of counts in the tritiated penguins' blood and the field stock dilutions.

Sizes of the penguins' body-water pools at initial capture were estimated from levels of HTO in the blood samples taken after a 2 hour isotope equilibration period (see Chapter 3). Rates of water intake while the penguins were away from the colonies were estimated from the dilution of HTO in the blood samples (Nagy and Costa 1980; equation 4), assuming a constant relationship between pool size and body mass. To improve the accuracy of the prey consumption estimates, several adjustments were made to the water intake rates. Firstly, the water influx estimates were increased by 7% to account for the degree by which the HTO technique under-estimates dietary water consumption by emperor penguins (an average of values in Robertson and Newgrain 1992, and the results presented in Chapter 3). Secondly, I subtracted 2.4 $mL/kg{\cdot}d^{-1}$ (the rate of seawater intake measured by Robertson and Newgrain 1996) from the water influx rates in an attempt to account for incidental seawater intake by foraging penguins. Since the penguins were not fasting, I assumed that their water requirements were met solely by their dietary water intake (i.e. snow consumption was negligible). Because the birds gained mass while at sea, and because tissue stored during the isotope integration period is not labelled with HTO, I deducted the estimated nonlabelled water from the total water intake for each penguin. To do this, I determined each penguin's mass gain (minus the mass of the stomach contents), assumed the increase in mass was fat, and assumed that when oxidised, 1 g of fat released 1.07 mL of metabolic water (Schmidt-Nielsen 1975).

To convert water intake per day away from the colony, to water intake per foraging day, two further adjustments were made. Firstly, I calculated the number of actual foraging days by subtracting the days of travel across the fast ice and other non-foraging days (determined from the TDRs) from the total number of days in a foraging trip. Secondly, I accounted for dilution of the HTO by metabolic water released from body tissues while the penguins commuted to and from the ice-edge; I assumed commuting penguins metabolised only fat and that each gram of fat yielded 39.4 kJ of energy (Groscolas et al. 1991) and the quantity of metabolic water previously mentioned. Based on the net specific cost of transport by a 23–30 kg emperor penguin (17.5 $J/kg{\cdot}m^{-1}$; Dewasmes et al. 1980) and the distance travelled to and from the ice-edge (80 km each way in the winter of 1993; as determined from satellite images), the metabolic water released was 3.67 L; this was subtracted from each bird's total water intake while away from the colony.

To estimate the water content of the diet, the chemical compositions of the fish, squid, and crustaceans the penguins consumed were assumed to be similar to the mean compositions determined respectively for the fish *Engraulis japonicus capensis*, *Maurolicus muelleri*, *Sardinops ocellatus* (Jackson 1990), and *Arippus trutta* (Robertson and Newgrain 1992), the squid *Loligo vulgaris reynaudii* (Jackson 1990) and *Nototodarus gouldi* (Robertson and Newgrain 1992) and Antarctic krill (Jackson 1990; Ikeda and Kirkwood 1989; and Chapter 3). The potential metabolic water from these species was calculated from published values for the oxidation of fat (see above) and protein (0.5 mL/g, Schmidt-Nielsen 1975). Thus, the total water (free plus metabolic) yielded from the fish, squid, and crustaceans in the diet was 0.85, 0.88 and 0.87 mL/g, respectively. These values were weighted proportional to the contribution of each prey component to the diet, as determined from the prey hard-tissue assessment. The mean water content of the penguins' food was thus estimated to be 0.87 mL/g.

The metabolisable energy intake for an animal in energy balance provides an estimate of field metabolic rate (FMR). The metabolisable energy intake by the penguins was estimated from their prey consumption rates, the energy density of their diet and published values of the efficiency with which emperor penguins assimilate energy from their food. Energy density in the diet was measured from duplicate portions of the stomach content samples that were oven dried at 60°C to constant mass, pulverised, compressed into pellets, weighed and combusted in a ballistic bomb calorimeter. The energy assimilation efficiency of emperor penguins fed diets of fish, squid and krill are 81.8, 76.2 and 70.5%, respectively (Robertson and Newgrain 1992, and Chapter 3). When weighted in proportion to the contribution of the various prey to the diet, the energy assimilation efficiency of the penguins was estimated to be 73.7%.

4.2.6 Statistical analysis

All means are presented ± 1 standard deviation. Comparisons between colonies were made with unpaired student t-tests following F ratio tests and, for percentage data, arcsine $\sqrt{}$ transformation to homogenise the variances. To simplify the presentation, the critical values for statistical comparisons have been included in Appendix 4B, not in the text. Significance was tested to the $p < 0.05$ level.

4.3 Results

4.3.1 Instrument effects and data treatment

On their winter foraging trips, penguins carrying PTTs or Paddles (the latter failed to record any data but presumably affected the penguins foraging: see Appendix 4C) consumed an estimated 30% less prey per day, spent 11% more days at sea and gained only 42% of the mass gained by non-encumbered penguins and penguins fitted with TDRs (which had similar mass gains). Consequently, for the assessment of the birds' water turnovers, feeding rates, trip durations, and mass changes, only data from unencumbered penguins or penguins carrying only TDRs were considered. However, the dive records from the three penguins carrying both PTTs and TDRs were included in the assessment of the penguins diving behaviours. The effect of the PTTs and Paddles on the penguins' feeding rates, trip durations and mass gains can be assessed from data presented in Appendix 4B.

4.3.2 Body masses and trip durations

The mean body masses of female emperor penguins departing the Auster and Taylor Glacier colonies in late May were similar, averaging 25.4 ± 1.8 kg (Appendix 4B). Only two Auster and three Taylor Glacier penguins that were not heavily burdened (see above) were recaptured when returning to their colonies; masses gained by all these penguins were similar (5.6 and 6.0 kg by Auster birds, 5.4, 5.6, and 8.0 kg by Taylor Glacier birds). Several penguins carrying TDRs were resighted although not recaptured on their return. The mean trip duration by four TDR-bearing Auster penguins (76.5 ± 3.1 d) was significantly longer than the mean trip duration of four TDR-bearing Taylor Glacier penguins (70.8 ± 3.0 d; Appendix 4B).

4.3.3 Foraging locations

The PTTs on two Auster penguins functioned for 72% and 59% of the penguins' trip lengths. The third PTT failed when the penguin reached the ice-edge. After departing Auster, the two tracked penguins travelled in an east- northeasterly direction and took about 6 days to travel the 80 km to the edge of the fast ice. Satellite images of the Mawson Coast in June revealed that the continental shelf waters 80–240 km east of Auster were virtually free of thick sea ice (Figure 4.2a, b). On entering the water, both PTT-bearing penguins swam northwards for about 40 km then remained in a polynya approximately 90–110 km northeast of Auster until at least mid-July when both PTTs failed. After mid-July, developing fast ice reduced the extent of the polynya where the penguins were presumed to be foraging. By late July, a 5–20 km width of open-water, situated over the continental slope, separated the edge of the fast ice edge from pack ice regions to the north (Figure 4.2c). Penguins foraging at this time would have had to move further offshore, either within the polynya or into pack ice regions over the open ocean.

Female penguins departing Taylor Glacier in late May travelled in a north-northeasterly direction toward a large polynya (Figure 4.2b). This polynya remained recognisable in satellite images throughout the winter, although it contracted in late July (Figure 4.2c). The polynya was situated over water depths of 200–500 m.

4.3.4 Diving behaviour

General

TDRs were recovered from ten Auster penguins (83% of those equipped) and from four Taylor Glacier penguins (67% of those equipped). Four Auster penguins and one Taylor Glacier penguin carried TDRs that were programed to start recording when the birds reached the ice-edge and dived; the remaining TDRs were programed to commence recording at later dates. Three of the four Auster penguins (the fourth penguin returned to the colony for an unknown period

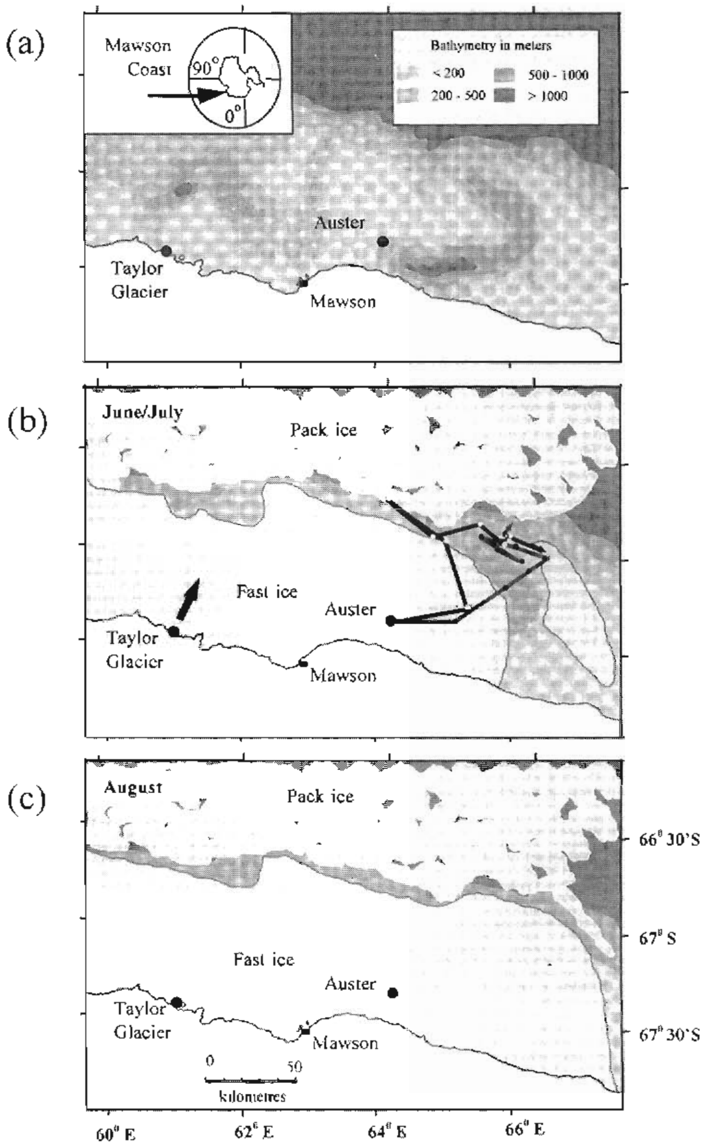

Figure 4.2 *(a) Mawson Coast of Antarctica, showing the location of the Auster and Taylor Glacier emperor penguin colonies, Mawson Station, and the topography of the seabed.*

(b) Sea ice conditions from late May to early July 1993, corresponding to the first two thirds of the female emperor penguins' winter foraging period. The paths of the two satellite tracked penguins from Auster are indicated by the black and grey lines extending from the colony. Dots along each line represents 4 day intervals. The arrow at Taylor Glacier shows the direction penguins took when leaving the colony.

(c) Sea ice conditions during late July and early August, corresponding to the last one third of the penguins' winter foraging period.

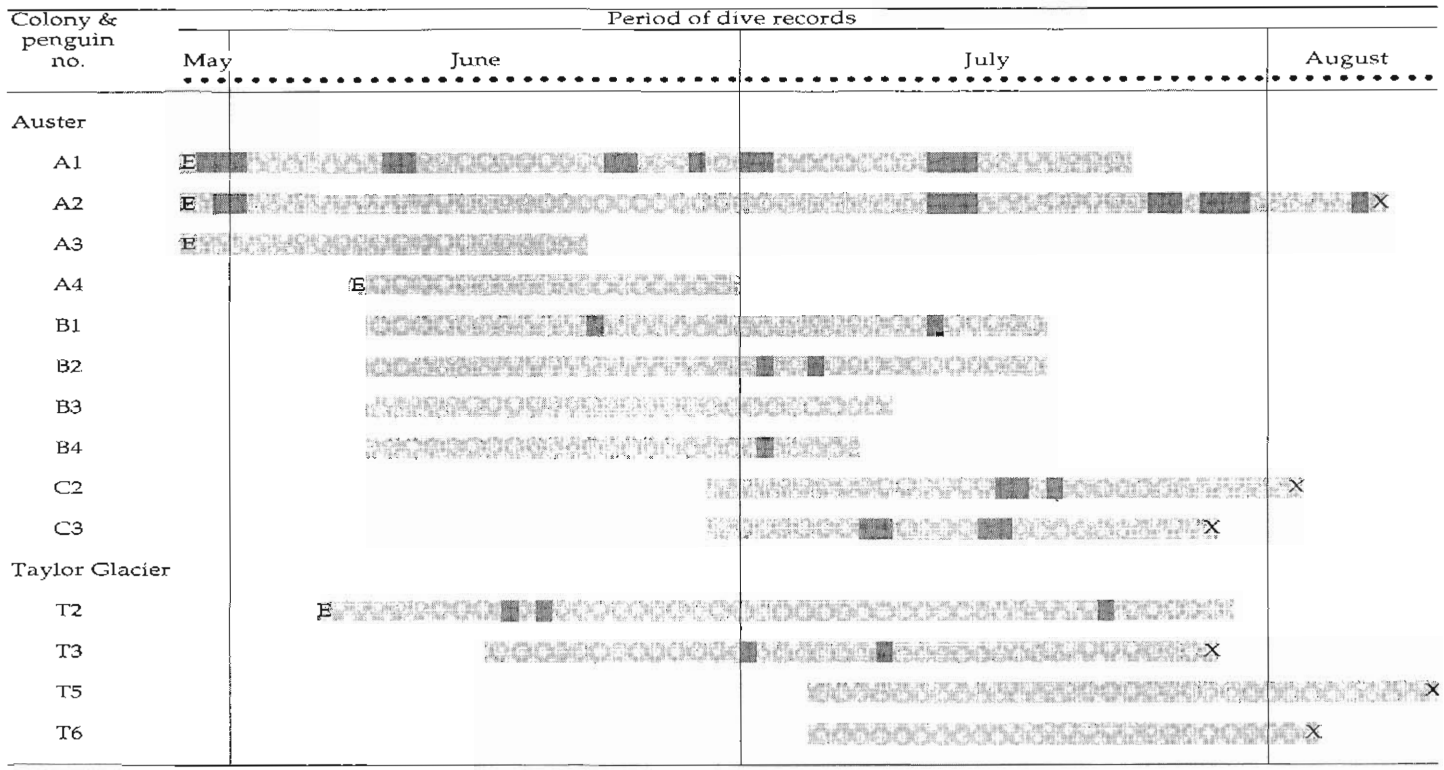

Figure 4.3 *Days at sea in the winter of 1993, recorded by time depth recorders (TDRs) fitted to 10 female emperor penguins from Auster colony and four from the Taylor Glacier colony. Records commenced when the TDRs were programmed to start, not necessarily when the birds reached the ice edge. Sampling ended when the TDR memories were filled; in most cases, this occured when the birds were still at sea. Dark shading denotes rest days (days spent at sea when the penguin did not enter the water); E denotes the first water entry and X denotes the last water exit for the foraging trip (when recorded).*

of time on release) took 8 days to travel the 80 km to the ice-edge; the Taylor Glacier penguin took 6 days to travel a similar distance to open water. Return journeys were recorded for only two Taylor Glacier birds which took 2 days and 6 days to reach the colony.

One TDR recorded data for a penguin's entire 71 days at sea, whereas the remaining 13 TDRs recorded periods of 23–56 d, equivalent to 30–70% of the penguins' days at sea (Figure 4.3). Data for a total of 542 days at sea were recorded.

While at sea, most penguins had days of no water entry, termed 'rest days'. Sometimes penguins rested on days when severe winds were recorded at Auster but overall there was no clear relationship between rest days and days of extreme weather. Auster penguins took more rest days than did Taylor Glacier penguins and, therefore, foraged on proportionally fewer of their days at sea (91.6 ± 7.4% and 97.3 ± 3.2% of days at sea, respectively) though the difference was not statistically significant. On average, penguins foraged on 93.2 ± 6.9% of their days at sea (both colonies combined, Appendix 4B).

During winter, temperature sensors in the TDRs recorded water temperatures between 0.8 and –1.8°C. Air temperatures were too low (<–2.3°C) to be recorded by the sensors but, at Auster, air temperatures were always below –10°C. Occasionally when the penguins were not in the water, and invariably at night, temperatures recorded by the TDRs rose above 10°C and at times to the sensors' upper limit (23°C) for several hours, indicating that the females huddled on the sea ice to keep warm (Figure 4.4). Although they were only rare events between foraging days, huddles did commonly occur between commuting days when penguins travelled across the fast ice between the colony and the ice-edge (see Chapter 6).

Daily foraging cycle

During the winter, penguins entered the water at 0930 ± 1.35 hours and exited at 1430 ± 0.97 hours (*n* = 14 penguins; 499 d; Figure 4.5). These times corresponded with just after dawn and immediately prior to dusk (when the sun was 3° below the horizon). On average, Auster penguins spent significantly less time in the water each day than did Taylor Glacier penguins (4.8 ± 0.1 hours and 5.4 ± 0.9 hours, respectively; Appendix 4B). This difference was mainly attributable to one Taylor Glacier penguin (T5 in Appendix 4B) that averaged 6.7 ± 1.7 hours in the water per day (*n* = 37 d). Excluding this bird's time, the mean time penguins from both colonies spent in the water each day was similar and averaged 4.8 ± 0.3 h/d, compared with a mean daylength of 3.4 ± 1.9 hours (*n* = 75 d) and a mean duration between dawn and dusk of 6.6 ± 1.1 h. In total, the birds spent 19.6% (2 350 of 11 976 hours recorded) of their time at the ice-edge in the water.

Most penguins swam at night at least once. A night swim usually consisted of 1–15 shallow dives (all <30 m depth), but one penguin (C2, Figure 4.3) performed 64 dives reaching a maximum depth of 60 m on the nights of 30 June and 1 July. These days coincided with rest days taken by two other penguins and the strongest wind conditions experienced for the year at Auster. In all cases of night diving, there was no indication that the penguins foraged. Night diving most likely resulted from accidental water entries, grooming, or swimming between ice-flows.

Diving behaviour

A total of 30 654 dives to depths greater than 10 m were recorded. Penguins from both colonies dived at a similar daily rate (62.3 ± 12.4 dives/d on average, n = 14 birds; Appendix 4B). The percentages of dives terminating at 10–20 m, 21 –50 m, 51 –100 m, 101 –200 m, 201 –300 m, and >300 m were 58%, 20%, 6%, 10%, 3%, and 1%, respectively, indicating a general decrease in dive frequency with increasing depth. Based on all dive profiles, 48% were non-foraging dives, 5% were search dives and 47% were feeding dives. The feeding dives accounted for 36% of the dives to <100 m and 84% of the dives to depths >100 m. Penguins from both colonies performed feeding dives at similar rates, the means of the pooled data being 25.9 ± 7.7 dives/d and 5.6 ± 1.4 dives/h (Appendix 4B). For all penguins combined, the ratio of asymmetrical: to ragged bottomed: to flat bottomed feeding dives was 50:43:7.

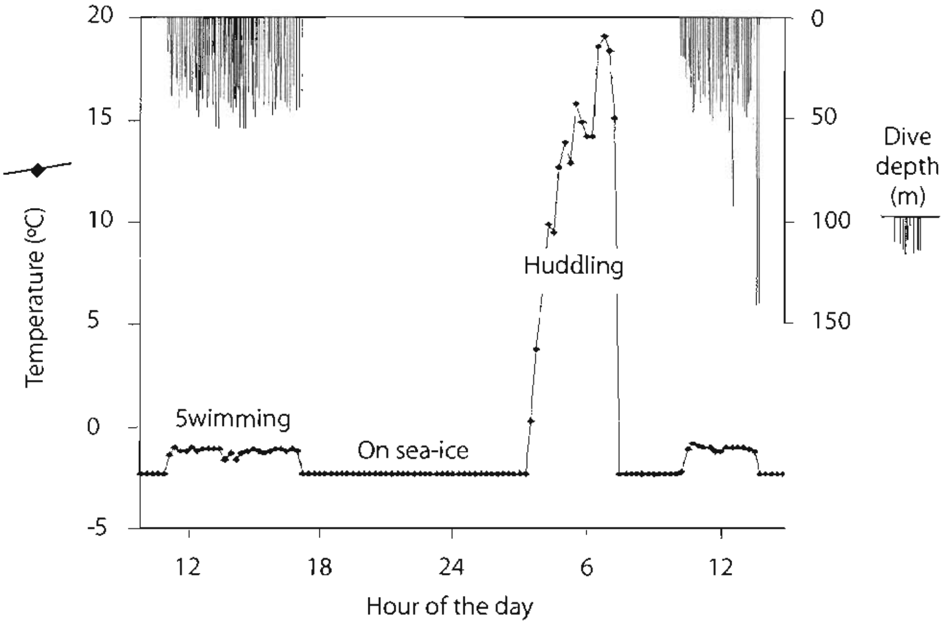

Figure 4.4 *Trend in temperature recorded by a time-depth recorder attached to a female emperor penguin foraging in mid winter. The figure shows temperature fluctuations when the penguin was swimming and when the penguin was assumed to be huddling with other birds on the sea ice. The temperature sensor did not record below -2.3°C.*

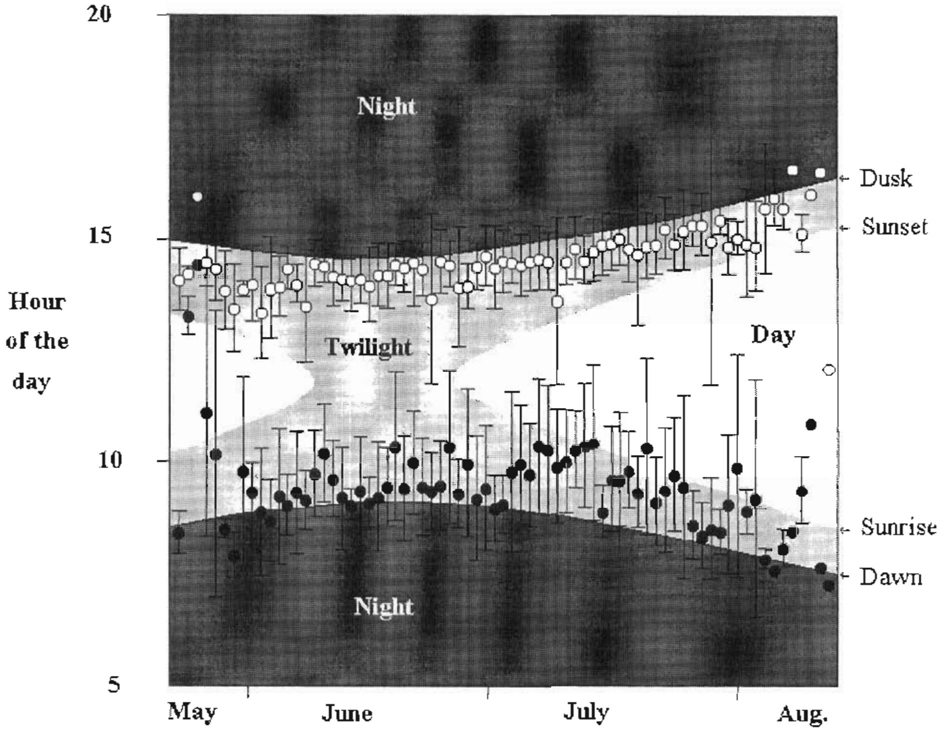

Figure 4.5 *Mean (±1 SD) water entry (closed circles) and water exit time (open circles) of 14 female emperor penguins that foraged along the Mawson Coast, Antarctica in the winter of 1993. Also shown are the periods of the night, twilight, and daylight. Twilight represents the times between civil dawn (when the sun is 3° below the horizon) and sunrise, and between sunset and dusk. Note that for a two week period in June, the sun did not rise above the horizon. All times preesented are local solar times (UTC plus 44 h).*

1 Feeding depths

Auster penguins dived to depths >100 m less frequently than did Taylor Glacier penguins. At Auster, the most frequented depth strata were 10–50 m, 100–200 m, and >300 m which were targeted on 32.6%, 33.3%, and 0.8% of the feeding dives, respectively. At Taylor Glacier, these depths were targeted by penguins on 50.1%, 9.9%, and 15.0% of the feeding dives, respectively. The mean maximum dive depth achieved by Auster penguins (335 ± 35.7 m) was less than that achieved by Taylor Glacier penguins (407 ± 70.3 m).

The 14 penguins from the two colonies were categorised into four groups based on their feeding depths (see Figure 4.6):

a) Shallow-depth foragers (Figure 4.6a). Two Auster penguins made 70.8% and 67.0% of feeding dives to depths of 10–50 m, and three Taylor Glacier penguins made 55.6 ± 2.1% of dives to these depths. The remaining nine penguins reached this depth range on 27.7 ± 7.7% (range: 13.8 to 35.6%) of their feeding dives.

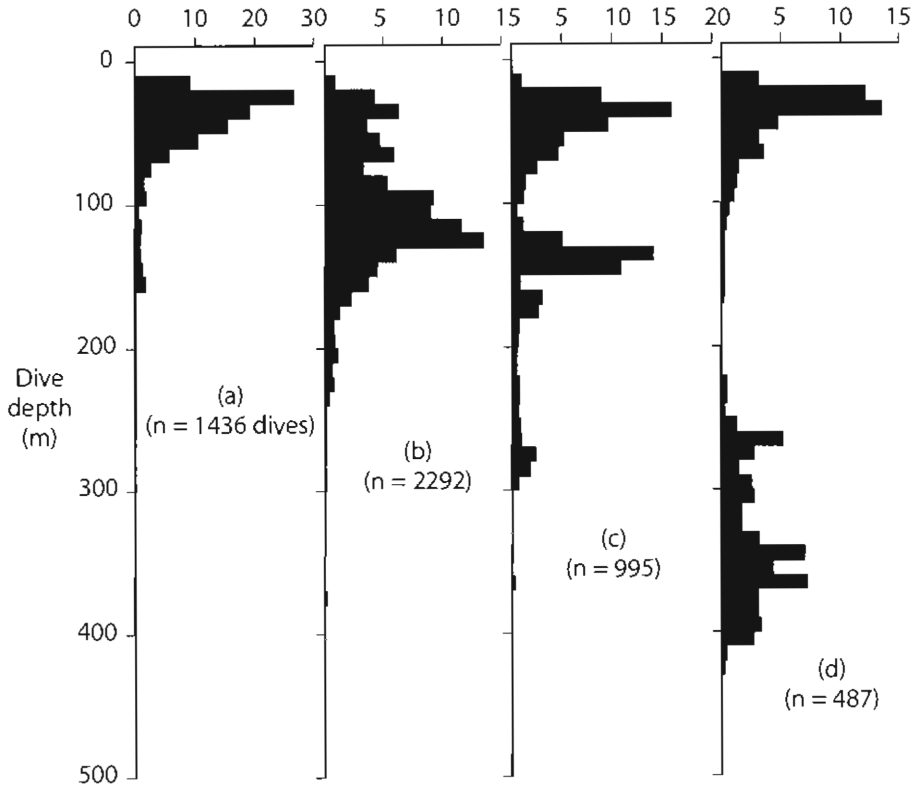

Figure 4.6 *Frequency distribution of the maximum depths of feeding dives made by four emperor penguins that had contrasting foraging patterns:*

(a) A1, a surface-forager from Auster;
(b) A2, a mid-water forager from Auster;.
(c) B2, a mixed-depth forager from Auster; and,
(d) T6, a deep-water forager from Taylor Glacier

b) Mid-depth foragers (Figure 4.6b). Three Auster penguins averaged 53.0 ± 5.2% of their feeding dives to depths between 100–200 m and only 18.6 ± 4.0% to the 10–50 m depth strata. The remaining 11 penguins conducted 19.2 ± 13.7% (range: 2.1 to 39.8%) of their dives to 100–200 m depth.

c) Mixed depth foragers (Figure 4.6c). Five Auster penguins conducted 32.1 ± 2.7% (range: 29.5 to 34.3%) of their feeding dives to depths between 10–50 m and 31.5 ± 7.7% (range: 24.3 to 39.8%) of dives to 100–200 m.

d) Deep foragers (Figure 4.6d). One Taylor Glacier penguin dived to depths >300 m on 40% of its feeding dives. Two Taylor Glacier penguins classed as shallow depth foragers also hunted below 300 m (7.5% and 12.4% of foraging dives) but the remaining 11 penguins rarely achieved these depths (0.7 ± 0.7% of dives; range: 0.0 to 1.9% of dives). For the three deep-diving penguins, the modal maximum depth of feeding dives > 300 m depth was 380 m.

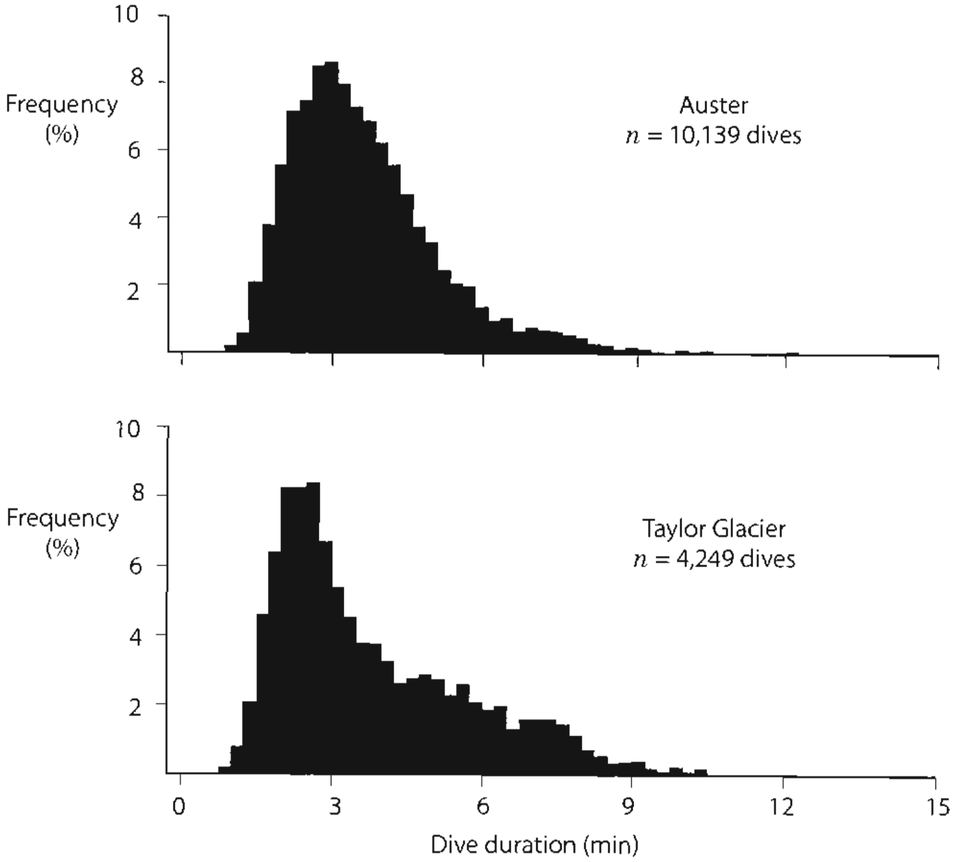

***Figure** 4.7 Frequency distribution of feeding-dive durations for 10 emperor penguins from Auster Colony and four penguins from Taylor Glacier Colony.*

During ascents from shallow dives (10–50 m depth), penguins often conducted brief descents that made their dive profiles appear asymmetrical. As a result, the penguins classed as shallow-depth foragers performed asymmetrical dives more frequently than did other penguins. The ratio of the three feeding-dive types (asymmetrical, symmetrical-ragged-bottomed and symmetrical-flat-bottomed) for shallow depth feeders was 20:10:1, whereas the comparable ratio for all other penguins was 4:5:1. Flat-bottomed dives by Auster penguins were performed at shallower depths and with less variation in depth (mean: 162.1 ± 23.3 m) than those of Taylor Glacier penguins (mean: 265.5 ± 55.9 m; Appendix 4B).

2 Feeding dive duration

The mean dive duration of the deep-diving bird from Taylor Glacier was 5.0 ± 2.2 min per feeding dive (n = 487 dives). The remaining three Taylor Glacier birds averaged 3.6 ± 0.2 min per dive which was similar to the durations by Auster birds (3.4 ± 0.2 min, n = 10 penguins; Appendix 4B and Figure 4.7). The calculated aerobic-dive limit of emperor penguins (5 min; Kooyman and

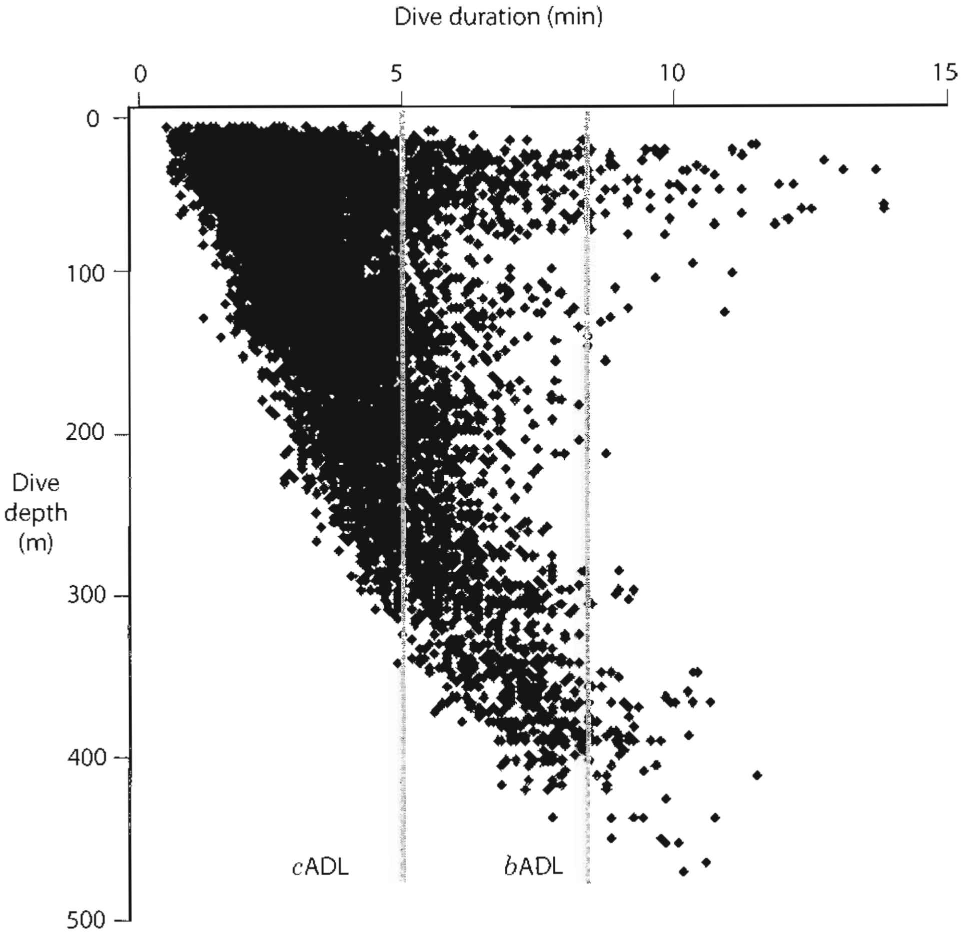

***Figure 4.8** Depth and duration of the feeding dives (n = 14,418) recorded for 14 emperor penguins from Auster and Taylor Glacier colonies in relation to the 5 min calculated Aerobic-Dive limit (cADL) and the 8 min behavioural Aerobic-Dive Limit (bADL) for emperor penguins (Kooyman & Kooyman 1995).*

Kooyman 1995) was surpassed on 10% and 25% of feeding dives by Auster and Taylor Glacier penguins respectively, including on all dives to depths >350 m (Figure 4.8). The behavioural aerobic-dive limit (8 min; Kooyman and Kooyman 1995) was surpassed on 0.8% and 3.2% of feeding dives by penguins from the respective colonies.

The duration of the longest dive achieved by individual penguins did not differ between colonies and averaged 12.0 ± 1.9 min (range: 8.8 to 15.2 min; Appendix 4B). Deeper-diving penguins did not necessarily achieve the longest dive durations; for example, the longest dive duration performed by the deep-diving Taylor Glacier penguin was only 10.7 min. Long duration dives were commonly performed at depths <100 m.

3 Bottom time and wiggles

Bottom times (when penguins were assumed to be foraging) of penguins from both colonies were similar and averaged 1.2 ± 0.1 min, equivalent to about one-third of the dive time. The deep-diving penguin averaged 1.6 min at the bottom of its dives. Because penguins performed a mean of 26 foraging dives/d, they spent approximately 30 min each day (i.e. 26 x 1.2 min) pursuing prey and feeding.

The penguins performed wiggles during 3403 feeding dives (24% of total feeding dives); the depths of these dives differed between colonies. Auster penguins performed wiggles mainly at 100–150 m depths (60% of all dives to these depths containing wiggles) but also at 20–30 m and to a lesser extent at 220–260 m depth (Figure 4.9). In contrast, Taylor Glacier penguins rarely performed wiggles at depths between 100-150 m, but mainly performed wiggles at 20–30 m, 260–290 m and 320–360 m (Figure 4.9).

Temporal changes in foraging strategy

During each day, the penguins' foraging patterns changed with deeper dives achieved when light was most intense. In periods of twilight the penguins rarely dived below 200 m however; around solar noon the birds commonly dived below this depth (Figure 4.10).

Throughout the winter the hourly dive rate remained constant (Figure 4.11a) but the time available to dive varied. As daylength increased after mid-July (see Figure 4.5), the penguins spent more time in the water (Figure 4.11b) and increased their number of dives per day (Figure 4.11c). Foraging effort (including the number of feeding dives per hour) also tended to peak when the moon was full (Figure 4.11), although a lunar effect on the number of dives per hour was not apparent in early August. During this time, satellite images of the penguins' presumed foraging area and weather observations at Auster colony did not reveal excessive cloud cover that might have reduced the lunar effect, the only anomalous weather pattern being a high-pressure system over the area.

Individual penguins displayed a range of foraging patterns; contrasting examples of which are shown in Figure 4.12. Most Auster penguins fed at two or more depth strata, targeting prey at these strata either on the same day or by switching their hunting over time from one depth strata to another (Figure 4.12a). By contrast, several penguins fed exclusively on prey at 0–70 m depth (Figure 4.12b), whereas others exclusively hunted prey at around 100 m (Figure 4.12c). Another penguin spent most of the winter foraging at a range of depths between 10–250 m rather than concentrating on prey at particular depths within this range (Figure 4.12d). All four Taylor Glacier penguins fed frequently at depths <100 m. One penguin fed almost exclusively at these depths (Figure 4.12e), whereas the others also foraged extensively at depths >200 m (Figure 4.12f).

The combined dive frequencies for Auster penguins revealed that, during June and early July, the birds concentrated their feeding dives at around 100 m depth and, to a lesser extent, at around 50 m depth. After mid-July, however, their hunting was concentrated at depths of around 50 m and less frequently at 150 m (Figure 4.13a).

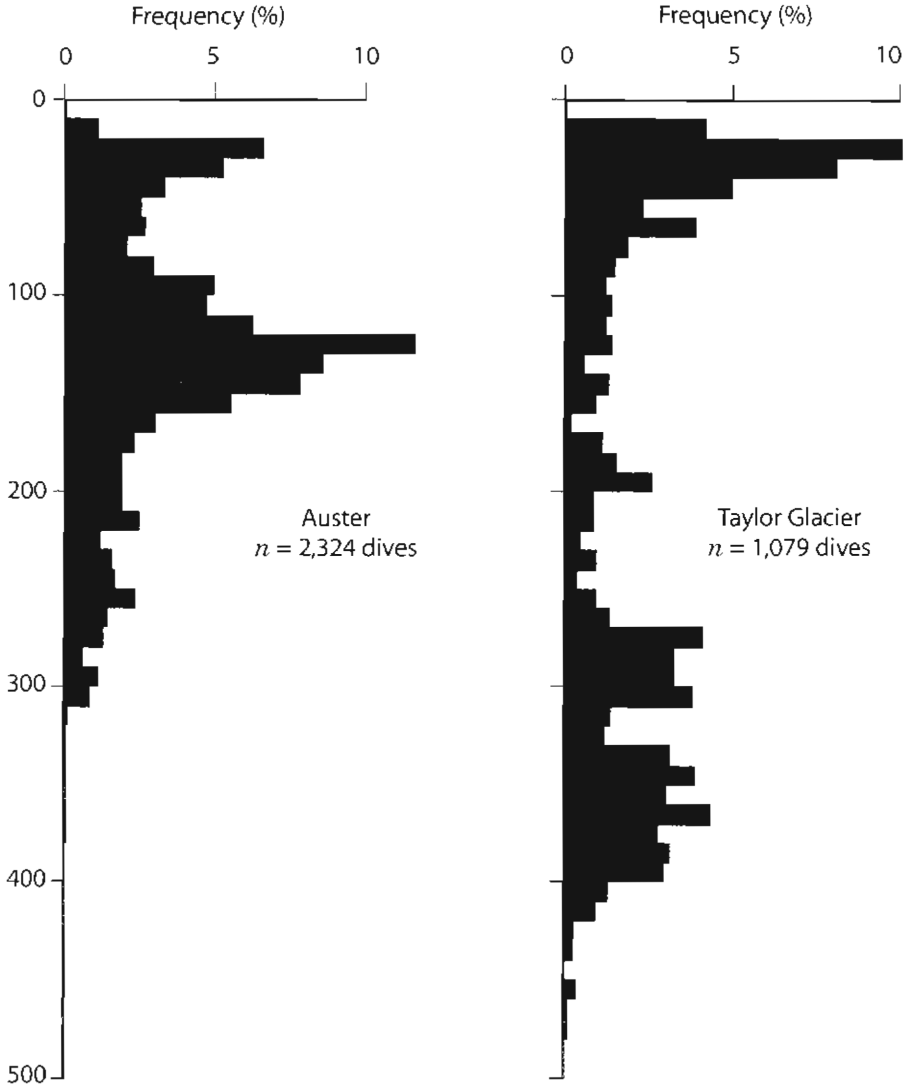

Figure 4.9 *An inter-colony comparison of the depth frequency of feeding dives containing "wiggles" (depth fluctuations presumed to be associated with feeding). Included are dives from 10 Auster and four Taylor Glacier penguins.*

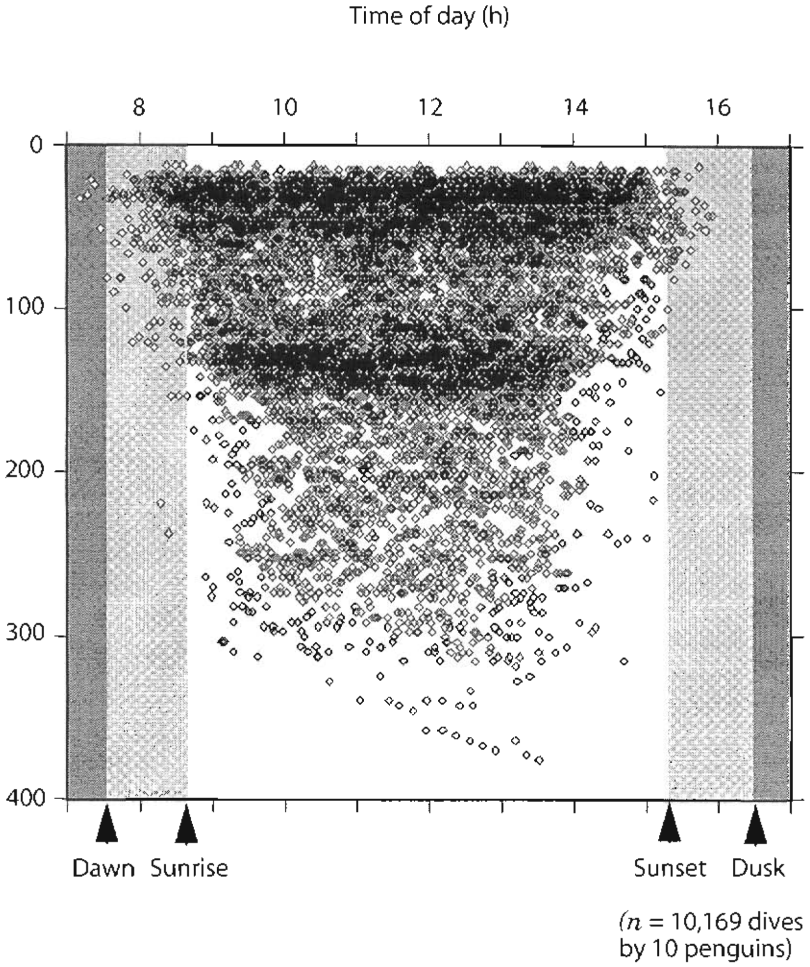

Figure 4.10 *Depth of feeding dives relative to time of the day (local solar time), recorded for 10 Auster penguins. Times of dawn, sunrise, sunset, and dusk are for the longest day (8 August 1993) during the sample period. Darker shading represents night, lighter shading represents twilight, and no shading represents daylight.*

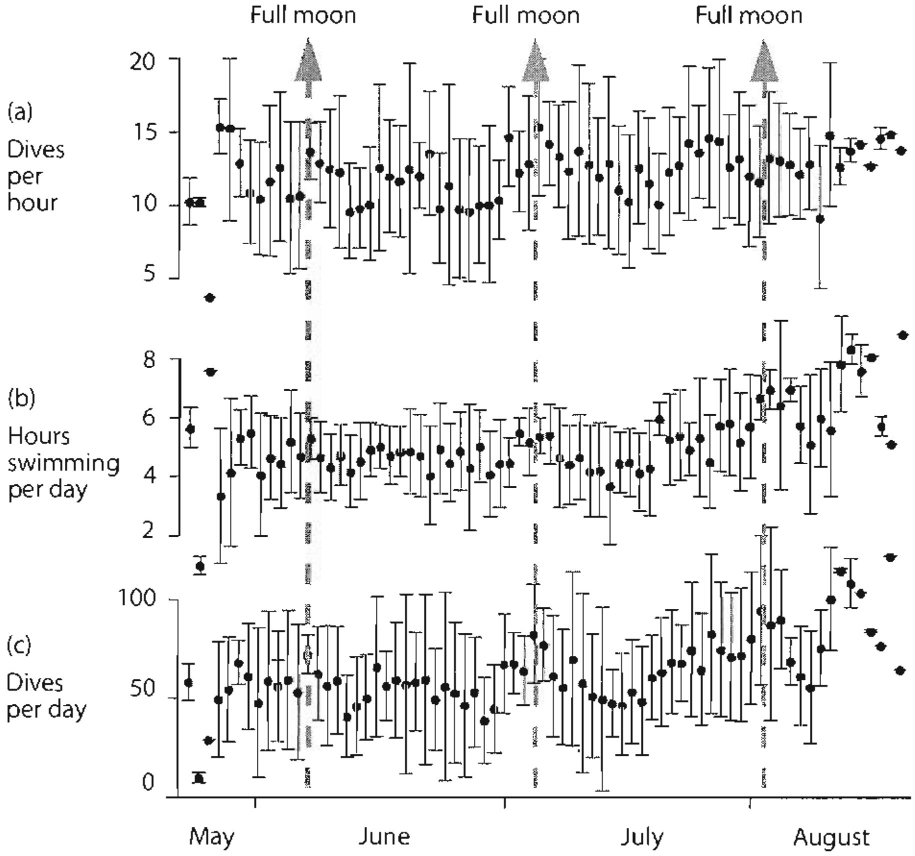

Figure 4.11 For Auster and Taylor Glacier birds combined, the mean number (± 1 SD) of dives per hour (top), hours swimming per day (middle) and dives per day (bottom), as a function of time at sea. Note that after mid-July, the number of dives/h remained constant, whereas daily swim time and dives/d increased corresponding with an increase in day length. Values for all measures were greatest when the moon was full.

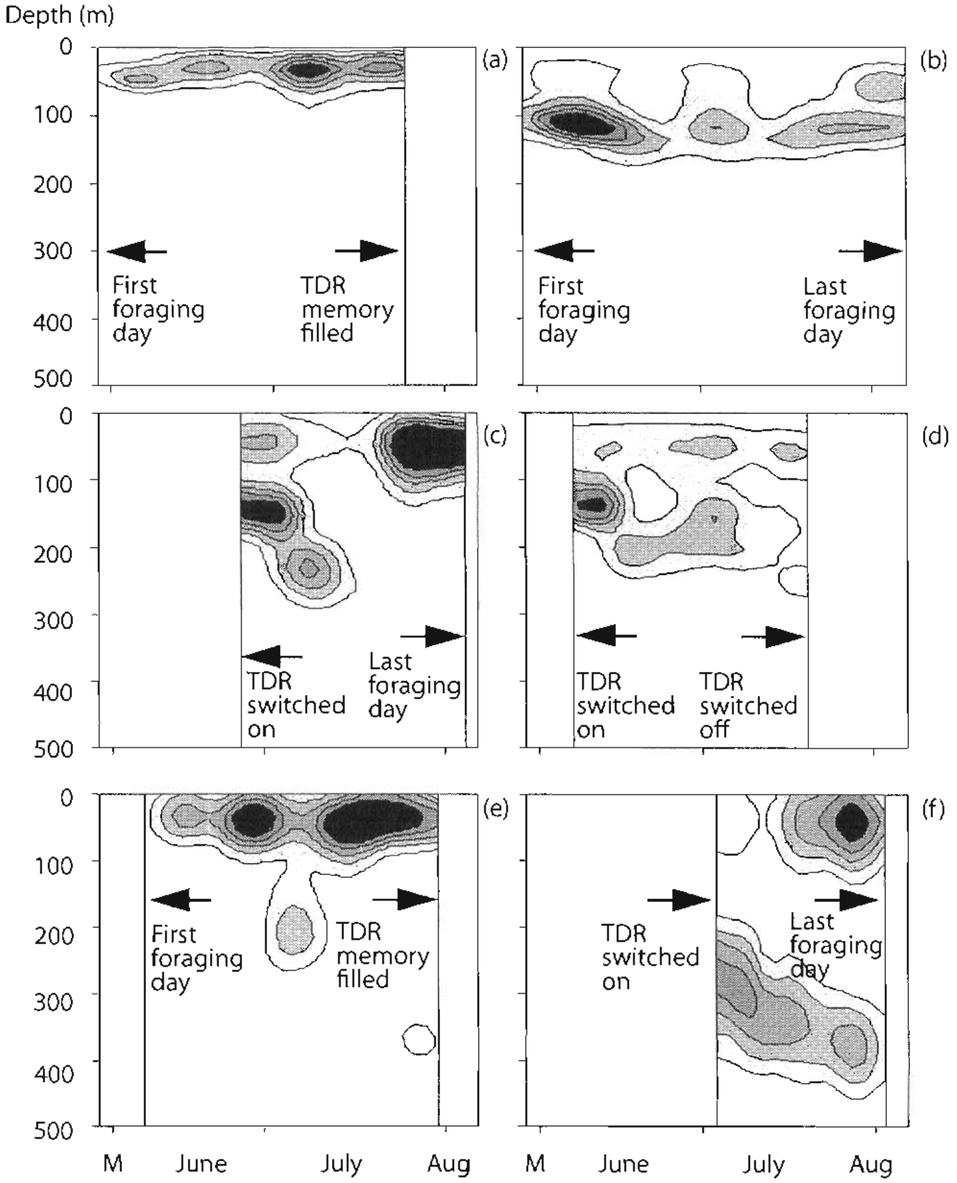

Figure 4.12 *Frequency distribution of maximum depths of feeding dives of emperor penguins from Auster (a-d) and Taylor Glacier (e-f). The figures are produced from Systat Graphics (Evanston, Illinois) using contour plots and kernel density estimators, which indicate data concentrations in the plot. The darker the shading, the greater the density: the lightest shading bound by the 5% contour and the darkest shading is bound by the 25% contour. Boundaries of each data set are indicated (TDRs are time depth recorders).*

(a) Penguin A1 foraged ony above 100m in depth
(b) Penguin A2 foraged around 100m in depth *(continued opposite)*

(c) Penguin C3 foraged in late June above 100 m and between 100-200 m, in early July mainly foraged >200 m and in late July at<100 m in depth, an overall pattern typical of about 50% of Auster penguins that carried TDRs.
(d) Penguin B11 foraged in early June at 100-200 m depth, and for the remaining period recorded, did not concentrate on any particular depth strata.
(e) Penguin T3 remained above the 100 m depth with occasional deeper forays.
(f) Penguin T6 foraged at depths <100 m and >200m; with time, the shallow dives became more frequent and the deep dives became deeper as the penguin may have been moving into deeper water.

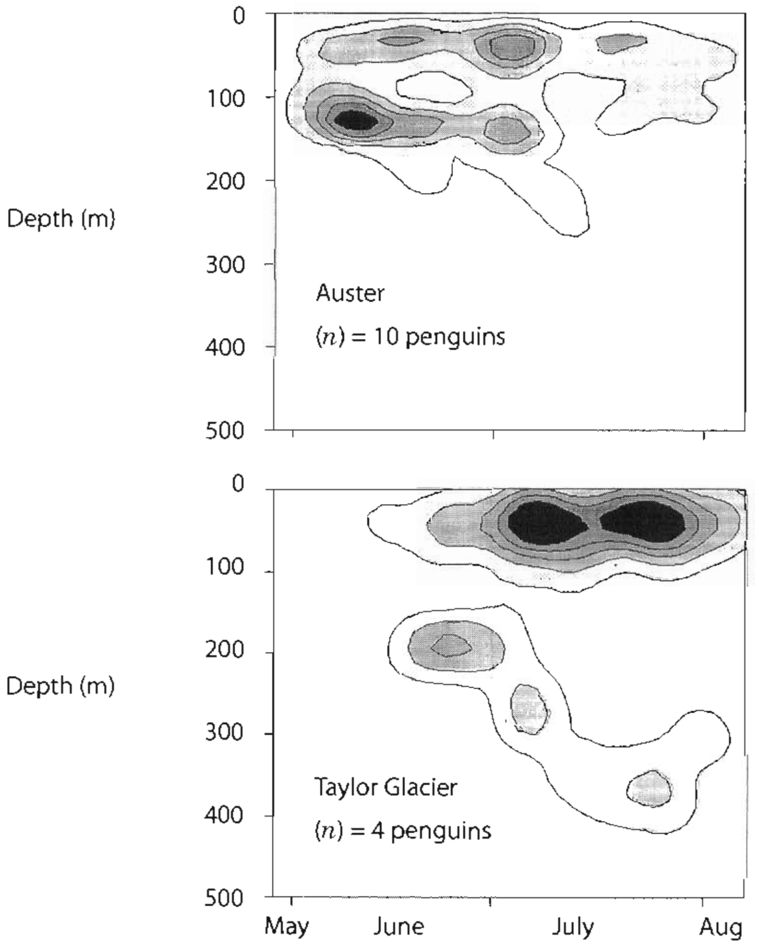

Figure 4.13 *Frequency distribution of feeding-dive depths in winter for 10 Auster penguins and four Taylor Glacier penguins. The lower frequency of feeding dives by Auster penguins late in winter, and by the Taylor Glacier penguins early in winter reflects the proportional lack of data for these periods compared with the data coverage at other times (see Figure 4.3; data are presented as per Figure 4.12).*

The Taylor Glacier penguins in June to early July fed most frequently to depths around 50 m and 200 m, and in late July they fed most commonly at around 50 m depth and occasionally hunted at depths >300 m (Figure 4.13b).

4.3.5 Dietary composition

The stomach-flushed Auster penguins (n = 17) had a mean body mass of 31.7 ± 1.9 kg and contained in their stomachs 766.9 ± 352.3 g wet mass (equivalent to a dry mass of 221.4 ± 104.9 g) of prey remains. Nine of the samples were heavily digested, seven were moderately digested, and one was lightly digested. In addition to prey components, the stomachs contained a mean of 7.8 ± 10.7 stones (5.8 ± 5.9 g per stomach).

Fish jaws were present in 13 (76%) of the subsamples and of the 23 fish recorded, 91% were Antarctic silverfish (*Pleuragramma antarcticum*). Otoliths were found in all of the subsamples and represented 125 individual fish of which Antarctic silverfish accounted for 97% (102) of the identifiable fraction (Table 4.1). Although more fish were represented by their otoliths than their jaws, smaller otoliths were too eroded to measure; hence only jaw lengths were used to determine the masses of Antarctic silverfish in the diet. The mean standard lengths and masses of silverfish were 83.0 ± 16.4 mm (range: 59.9–115.9 mm, n = 16) and 4.29 ± 2.84 g (range: 1.32–10.89 g). The mass of a single *Trematomus* sp. (87 g) was calculated from otolith length, assuming that the fish was a *T. eulepidotus* (the most likely species based on otolith shape). Masses of an unknown nototheniid and an unknown channichthyid were assumed to be the same as the unidentified *Trematomus* (87 g). Unknown fish in the samples were probably silverfish with some other nototheniids also present and were assumed to have mean masses of 10 g. Based on the calculated masses, fish contributed 27% by mass to the penguins' diet (Table 4.1).

Squid beaks occurred in seven (41%) of the subsamples, with a total of 16 individual squid represented; 11 glacier squid (*Psychroteuthis glacialis*), four *Kondakovia longimana* and one *Alluroteuthis antarcticus* (Table 4.1). All but one of the beaks were too eroded to measure for the prey mass calculations. The only measurable beak came from a glacier squid with a mantle length of 163 mm and a mass of 91 g. A sample size of one is too small to use for any assessment of the squid mass in the diet, so three additional, non-eroded, glacier squid beaks were selected at random from the unsorted portion of the stomach samples. The mean mantle lengths and masses of the four squid measured were 176 ± 16 mm and 110 ± 23 g, respectively. Overall, squid represented only 3% of the prey mass of the penguins' diet (Table 4.1).

Crustacean fragments were present in 88% of the subsamples, with all identifiable parts being Antarctic krill. A total of 3 894 krill was recorded. Assuming that the mean mass of each krill was 0.6 g, the krill component was 70% by mass of the penguins' diet (Table 4.1).

In summary, the penguins' diet comprised 27% fish, 3% squid and 70% krill. The energy density of the diet averaged 5.13 ± 0.27 kJ/g wet mass (n = 12 stomach samples).

Table 4.1 *Prey composition in 300-g subsamples of stomach contents from 17 female emperor penguins returning to Auster colony in late July/early August, based on frequency of occurrence in samples, quantification of the prey by numbers, and quantification of the prey by proportional masses.*

Prey species	**Samples containing prey**		**Prey composition**			
			[a]By item		**[b]By mass**	
	n	*(%)*	***n***	*(%)*	**g**	*(%)*
Fish						
Nototheniidae						
Pleuragramma antarcticum	15	(88)	102	(2.5)	438	(13)
Trematomus sp.	1	(6)	1	(0)	87	(2.5)
unknown nototheniid	1	(6)	1	(0)	87	(2.5)
Channichthyidae						
unknown channichthyid	1	(6)	1	(0)	87	(2.5)
Unknown fish	11	(65)	20	(0.5)	200	(6)
Total	17	(100)	125	(3)	899	(27)
Squid						
Psychroteuthis glacialis	6	(35)	1	(0)	110	(3)
Alluroteuthis antarcticus		1	(6)			
Kondakovia longimana	2	(12)				
Total	7	(41)	1	(0)	110	(3)
Crustacean						
Euphausia superba	15	(88)	3894	(97)	2336	(70)

[a] *Fish are represented by otolith pairs, squid by non-eroded lower beaks and crustaceans by pairs of eyes.*

[b] *Mean mass was calculated as follows; from jaw lengths of Antarctic silverfish* (P. antarcticum, *4.29 g), from otolith length for* Trematomus sp. *(potentially* T. eulepidotus, *87 g), as for* Trematomus *(87 g) for the unknown nototheniid and channichthyid; and from the lower beak rostral length for glacier squid* (P. glacialis, *110 g). Mean masses of unknown fish (probably a mixture of mainly Antarctic silverfish and some other nototheniids) were assumed to be 10 g; Antarctic krill* (E. superba*) masses were assumed to be 0.6 g.*

4.3.6 Water influx and prey consumption rates

When departing their colonies in May, Auster penguins had significantly higher body water contents (601.6 ± 38.7 mL/kg, n = 25) than did Taylor Glacier penguins (525.0 ± 31.1 mL/kg, n = 6; Appendix 4B), indicating that Taylor Glacier birds were either fatter or more dehydrated than Auster birds. Of the 25 penguins injected that did not carry heavy devices, only two from Auster and three from Taylor Glacier were caught and sampled on their return to the colonies before they had fed their chicks. Between-colony comparisons of the water turnover rates of these penguins revealed no statistically significant differences (Table 4.2).

To calculate prey consumption rates per foraging day, non-foraging days were accounted for by subtracting travel days (8 days for the outward journey and 4 days to return) and rest days (8.5% and 2.6% of days at sea for Auster and Taylor Glacier penguins, respectively) from the time each penguin spent away from its colony. Accordingly, the penguins foraged on 56 ± 4 d. Water influxes per foraging day were 56.3 ± 0.6 mL/kg and 53.7 ± 6.9 mL/kg for Auster and Taylor Glacier penguins, respectively. The mean water influx of birds pooled from both colonies was 54.7 ± 5.1 mL/kg·d^{-1} (Table 4.2).

Based on these water influxes, and assuming that the diets of birds from Auster and Taylor Glacier had similar water and energy contents, penguins from these colonies consumed an estimated 65.0 ± 0.7 g/kg·d^{-1} and 62.0 ± 7.9 g/kg·d^{-1}, respectively (63.2 ± 5.9 g/kg·d^{-1} for all penguins combined). The combined value is equivalent to a daily intake rate of 1.8 ± 0.1 kg food for a 28.8 kg penguin (the mean mass of females) and a metabolisable energy intake of 238.9 ± 22.1 kJ/kg·foraging d^{-1} (Table 4.2). Hourly prey consumption by the penguins that carried TDRs was a mean 0.39 ± 0.05 kg (n = 4).

Individual penguins varied markedly in their foraging performance. For example, two Taylor Glacier penguins (T2 and T3 in Table 4.2) departed the colony with the same body masses (about 25 kg), gained the same mass while away (about 5.5 kg), and foraged at similar depths. However, one penguin consumed 1.7 kg/d, whereas the other consumed prey at the rate of 2.0 kg/d and returned to the colony 6 days before the slower consumer. Therefore, at the critical time of year when the fasting males need their partners to return to avoid chick abandonment, the female that ate at a faster rate was able to relieve her mate almost 1 week earlier than the female that ate at a slower rate.

4.4 Discussion

4.4.1 Foraging strategies of the females in winter

Probable foraging areas

The two satellite-tracked Auster females frequented waters in the region of the outer continental shelf and shelf slope approximately 90–110 km from the Mawson Coast (near 67°S; Figure 4.2). Circumstantial evidence suggests this area was favoured by many females in winter. Firstly, open water existed over the slope region for the duration of the females' time at sea. Secondly, the complex marine topography (ranging from 100 m to 1000 m water depth) of

Table 4.2 *Prey consumption rates and metabolisable energy intake by individual female emperor penguins (B1, E4, etc.) foraging in winter.*

Colony	Penguin number	Mean mass (kg)	Mass gained (kg)	Trip duration (d)	[a]Water intake (mL/kg.d^{-1})	[b]Water intake per foraging day		[c]Prey consumption per day		[d]per hour (kg)	[e]Metabolisable energy intake (kj/kg.d^{-1})
						(d)	(mL/kg)	(g/kg)	(kg)		
Auster	B1	28.8	5.6	78	45.5	60	56.7	65.5	1.9	0.41	247.5
	E4	27.0	6.0	73	44.6	56	55.8	64.5	1.7		243.8
	Mean	27.9	5.8	76	45.0	58	56.3	65.0	1.8		245.6
	±SD	1.3	0.3	4	0.7	3	0.6	0.7	0.1		2.6
Taylor Glacier											
	T2	27.8	5.5	74	41.8	57	52.2	60.3	1.7	0.34	228.0
	T3	28.4	5.4	67	47.9	50	61.2	70.6	2.0	0.42	267.1
	T6	31.9	8.2	72	37.9	55	47.7	55.0	1.7	0.34	208.1
	Mean	29.4	6.4	71	42.5	54	53.7	62.0	1.8	0.36	234.4
	±SD	2.2	1.6	4	5.0	3	6.9	7.9	0.2	0.05	30.0
[f]Both colonies combined											
	Mean	28.8	6.1	73	43.5	56	54.7	63.2	1.8	0.38	238.9
	±SD	1.9	1.2	4	3.8	4	5.1	5.9	0.1	0.04	22.1

[a] *Water turnover estimated from tritium dilution rates (See Nagy & Costa 1980) and was adjusted to take into account a seawater intake of 2.36 mL/kg body mass per day (see Robertson 1994), an inherent underestimate in the tritium technique of 7% (See Robertson & Newgrain 1992, and chapter 3), and subtraction of 1.07 mL per gram of mass gained (mass change minus mass of stomach contents), which assumes that all mass gained was fat and that water in this fat did not pass through the body water.*

Caption comtinues on page 70

[b] *Foraging days equal trip duration minus non-foraging days (travel over fast ice & rest days). Metabolic water released during travel (3.67 L) was subtracted from the total water intake.*

[c] *The proportion of free plus metabolic water in the dietary mix is 0.87 mL/g. Daily prey consumption is presented as g of prey/kg of the penguin's body mass, then kg of the prey/penguin.*

[d] *The hourly prey consumption calculated for penguins with TDRs which recording swimming time per day.*

[e] *Calculated by multiplying mass specific prey consumption rates by the penguins' mean assimilation efficiency (73.7%) and the energy content of the diet (5.13 kJ/g).*

[f] *There were no statistically significant between-colony differences (t-tests).*

the slope provided the penguins with a range of foraging habitats in a region of potential nutrient upwelling and high productivity. Thirdly, during the last weeks of winter foraging, females from Auster ate Antarctic krill, Antarctic silverfish, and glacier squid. Antarctic krill aggregate in the vicinity of the continental slope (Miller and Hampton 1989), whereas Antarctic silverfish and glacier squid are most abundant in the mid-water ecosystem of the outer continental shelf (Hubold 1984, Lu and Williams 1994). Although foraging locations of the female penguins requires further research, the evidence suggests that large numbers of birds foraged in the vicinity of the shelf break within approximately 100 km of Auster during the 1993 winter.

Taylor Glacier females may also have foraged in the vicinity of the shelf break. When leaving the colony after egg-laying the females headed in a N-NE direction toward the largest area of open water near the colony, a recurring polynya (a regular feature of the Mawson Coast sea ice) that extended south from the slope polynya and was situated over the outer continental shelf (Figure 4.2b). Presumably a large proportion of the Taylor Glacier birds foraged in the vicinity of this polynya during winter, suggesting that they, too, need not have travelled more than approximately 100 km from their colony.

The females had about 9 weeks between when they departed and when they needed to return to the colony, and to forage at distances far greater than 100 km from the colony is not beyond their capabilities. In summer 1990, an emperor penguin in the Ross Sea travelled 500 km during a 4 week foraging trip (Ancel et al. 1992). Moreover, Adélie penguins (*Pygoscelis adeliae*), just one-sixth the mass of emperors, often travel >100 km from their colony during foraging trips of <3 wk duration from colonies on the Mawson Coast (Kerry et al. 1995a) and king penguins (*Aptenodytes patagonicus*), half the size of emperors, can travel >500 km during foraging trips that are <3 wk long (Jouventin et al. 1994). The emperor penguin's potential foraging capabilities, combined with evidence that the Auster females did not actually travel far, suggest that they could catch sufficient prey close to their colony.

Limited foraging time

The daily activity cycle of the female emperors was dictated by the short day-lengths in winter. Each foraging day, the birds were in the water for approximately 5 hours, coinciding with the period of daylight, and spent the remaining 19 hours per day on the sea ice. Like other penguin species (see Wilson et al. 1989a, Wilson et al. 1993), emperor penguins presumably forage by sight. This limits them to foraging in daylight, twilight, or when the moon is full. Despite having just 5 hours per day in which to forage, the females further reduced their overall foraging effort by engaging in "rest days", when they did not enter the water. Rest days may have been taken when rough, ice-laden seas or the sighting of nearby predators overcame the penguins' motivation to feed. Rest days may also have been spent searching for open water after surface waters near the penguins froze at night. Such occurrences, however, seem unlikely to have caused the loss of many entire foraging days, although they could explain why the water entry times were more variable than the water exit times (see Figure 4.4). The prevalence of rest days (23% of one bird's days at sea), along with the birds' gains in body mass (6 kg, a 25% increase) while at sea, suggests that prey were sufficiently abundant and easy to gather to allow penguins to take rest days without compromising their condition, and that the penguins were not pushed to the limit to fulfil their food requirements during winter.

Spatial and temporal variation in prey distribution

Apart from differences in the daily dive times, the foraging behaviour of female emperor penguins in winter was similar to that of male and female emperors in other studies during spring and summer (Ancel et al. 1992, Robertson 1994, Kooyman and Kooyman 1995). The impression that emerges is a dive repertoire dominated by feeding dives to modal depths of 0–70 m and 90–180 m, with maximum depths of 375–534 m, modal dive durations of 3–6 min, and maximum dive durations of 15–22 min. In addition, bottom times commonly constitute about 30% of dive times. The similarities between the penguins' diving behaviours at different times of year and at different locations suggests uniformity in prey types (pelagic and bentho-pelagic species), foraging environments (water depths of 100–600 m and a variable sea-ice cover), and the penguins' hunting abilities. Emperor penguins can forage in a greater range of depths and can be submerged for longer durations than any other seabird (Kooyman 1975, 1989, Kooyman et al. 1992, Chappell et al. 1993, and references therein); among air breathing tetrapods, only phocid seals and whales compete with emperors for the same prey species at depths below approximately 200 m.

The emperor penguins' ability to attain depths >300 m in winter demonstrates that their deep diving is not inhibited by the low light levels at this time of year. The purpose of deep dives by emperor penguins may be to gather gastric stones (which presumably aid digestion), to locate the bottom for navigational purposes or to hunt prey that live at depth. During chick feeding, emperors incidentally pass on their gastric stones to chicks and may need to replace these stones regularly (Kooyman and Kooyman 1995). However, the prevalence of deep dives in winter, when chicks are not fed and gastric stones presumably endure in the adult's stomach, suggests deep dives serve a different purpose than to find stones. The penguins may dive deeply to determine their location, to assess the depth of the water column or to locate sea-mounts where food might be plentiful. Alternatively, during deep dives the emperors may hunt prey that occur only at depth and/or are most easily caught there. Deep dives would be energetically expensive compared to shallow dives but would nevertheless be energetically profitable if associated with the capture of a large-bodied prey (Costa 1991). I suspect a dual purpose—that deep dives are a foraging technique that aids navigation and provides the opportunity to capture large-bodied prey.

The frequency of the emperor penguins' dives to particular depths coupled with the likely distribution of the main prey, krill and Antarctic silverfish, provide insights into the prey distribution. In summer, the greatest densities of krill are found at 0–70 m depth (Siegel 1985, Higginbottom and Hosie 1989, Godlewska 1993), although aggregations may form directly under the sea ice (O'Brien

1986, Marschall 1988) and near the seafloor (Kawaguchi et al. 1986, Duhamel and Williams 1990). In winter, krill-eating gentoo penguins (*Pygoscelis papua*) (Williams et al. 1992a) and crabeater seals (*Lobodon carcinophagus*) (Bengtson and Stewart 1992, Nordøy et al. 1995) forage between 0–90 m depth, suggesting that many krill congregate at these depths year-round. Antarctic silverfish of the standard length taken by the penguins (mean: 83 mm, fish ≥2 yr old) occur year-round over the outer continental shelf at 50–400 m depth and in the top 100 m in the open ocean (Hubold and Ekau 1987, Williams and Duhamel 1994). Consequently, Auster penguins could have hunted krill and silverfish at both 0–70 and 100–150 m depth strata (see Figure 4.13). On the shelf, silverfish may have been more abundant, but off the shelf break and in the open ocean it is likely that krill were the dominant prey at these depths. Taylor Glacier penguins could also have fed on krill and/or silverfish at the 0–70 m depth range, where most of their dives were concentrated. Apparently, though, these prey species were scarce at 100–150 m depth in the Taylor Glacier penguins' foraging grounds, since the penguins rarely frequented this strata. Instead, the penguins hunted at depths of 200–400 m , where krill and silverfish may have occurred but larger, more nutritious prey, such as squid or bentho-pelagic fish species, were more probably hunted to justify the energetic expense of deep diving.

As the winter progressed the penguins' deep diving (to depths >100 m) increased in depth and decreased in frequency, and the proportion of shallow dives increased. Perhaps developing fast ice over the continental shelf forced the birds to move further offshore and into deeper waters, where the penguins may have lost contact with, or depleted, the prey at depth, or located larger or more densely aggregated prey nearer the surface. Whatever the reason, the change suggests that many females foraged in different environments toward the end of their trips, and potentially further offshore than earlier in winter. The penguin for which an entire foraging record was obtained restricted its foraging effort to water depths of <100 m for the entire winter, suggesting that it foraged in the same environment all winter.

The change in foraging strategy over time highlights a limitation of dietary predictions based on samples taken at only one stage of a foraging trip (in this case, at the end). The dietary samples reflected the penguins' diet late in their trips. However, given that the two penguins tracked early in winter remained in open water over the slope where krill are abundant, and that >50% of the birds' dives at this time went to depths <100 m, where the greatest densities of krill presumably reside, krill probably were a major component of the diet throughout winter.

This is the second study of an antarctic seabird (see Williams et al. 1992a) to demonstrate a significant dependence on krill during winter. Prey consumption by each female over winter was estimated as the product of each bird's consumption rate per day away and the number of days spent away from the colony. Accordingly, in the winter of 1993, each female ate 101 ± 8 kg of prey, of which krill accounted for approximately 70% (70 kg, assuming that the diet throughout winter was relatively constant). The breeding population of females at Auster and Taylor Glacier (13 300 and 2 400 breeding pairs respectively;

see Chapter 2) would have consumed an estimated 1 330 and 250 metric tons of prey, respectively, of which approximately 930 and 175 metric tons, respectively, were krill. These amounts are substantial, considering that the females probably did not disperse widely to forage. Evidently krill can be an abundant and available prey species in antarctic waters, even in winter. In light of this appraisal, the main constraint on the breeding chronology of other krill-dependant bird species that breed in summer might be the short day-lengths of winter (limiting the time available for hunting), the distance between breeding areas and foraging grounds caused by the winter fast ice, and the effects of severe weather on the reproductive processes, rather than a shortage of food.

In 1988, the stomach contents of females returning to Auster after winter contained only small quantities of krill (Robertson et al. 1994a). Instead the penguins had eaten predominantly shelf-dwelling prey such as the bentho-pelagic fish *T. eulepidotus*, along with antarctic silverfish and glacier squid (40%, 26%, and 10% by mass, respectively), a diet that yielded 20% more energy per gram than the krill-based diet in 1993 (6.14 and 5.13 kJ/g, respectively). In both years, the penguins took the same route to and from the ice-edge and, although the extent of the fast ice differed between years, probably began and ended their foraging in the same general area of the outer continental shelf. That the penguins in 1988 ate bentho-pelagic and pelagic fish, whereas those in 1993 consumed mainly krill, suggests that prey availability and/or penguin foraging behaviour varies considerably between years. The capacity of emperors to switch prey presumably increases their tolerance to fluctuations in food supply that occur in antarctic oceans and that can afflict species such as gentoo and macaroni penguins that depend predominantly on krill (Croxall et al. 1988a).

Consumption rates and energy requirements

From the penguins' diving behaviours, diets, and prey consumption rates, it is possible to estimate their prey capture rates and energy requirements in winter. Prey capture rates were estimated by dividing the average daily consumption rate by the mean masses of the prey. Accordingly, on each foraging day, each penguin consumed the equivalent of about 420 antarctic silverfish or 2 250 antarctic krill, or some combination of both these species. Given that the penguins averaged 26 foraging dives per day, the mean number of prey caught per dive could be 115 krill or 16 silverfish. To catch 115 krill or 16 silverfish would presumably involve a dive to <150 m depth, and then a search and feeding period of about 1.5 min (the mean bottom time of foraging dives to <150 m). During foraging dives to depths >200 m, when the penguins presumably sought prey larger than krill and silverfish, successful prey captures need not have been as frequent as for shallow dives. For example, if the prey were *T. eulepidotus* of the mean size taken by emperors in the 1988 winter (130 g; Robertson et al. 1994a), the penguins would need to catch 14 fish per day, equivalent to one fish every second foraging dive, to achieve their mean daily prey consumption.

During winter, the females foraged for various reasons; to replenish energy reserves metabolised during the courtship fast, to fatten in preparation for the forthcoming chick-brooding fast, and to collect food for the chick. The food collected for the chick (0.77 kg) was minimal in comparison with the total prey intake of about 100 kg during the winter foraging trip, and could be caught in less than one day. This means that nearly all of the prey taken by the females was used for self-maintenance and to build tissue energy reserves in preparation for chick-brooding.

The calculated Field Metabolic Rate (FMR) of 239 $kJ/kg{\cdot}d^{-1}$ (Table 4.2) for a 29 kg emperor is only about 1.5 times the resting metabolic rate for emperor penguins (164 $kJ/kg{\cdot}d^{-1}$, an average of values in Le Maho et al. 1976 and Pinshaw et al. 1976), and is 40% lower than the FMR predicted for a 29 kg seabird in energy balance (384 $kJ/kg{\cdot}d^{-1}$, from equation 16 of Nagy 1987). The FMR seems low, considering that the birds spent almost 5 hours per day swimming and managed to add 6.1 kg in body mass while at sea. However, the resting metabolic rates measured previously (Le Maho et al. 1976 and Pinshaw et al. 1976) may be overestimated because the birds were caged and the stress of containment could have increased their metabolic rates. Also, the estimates of FMR (Nagy 1987) were based on seabirds actively feeding chicks in summer, when metabolic rates would be greater than for birds feeding mostly for self-maintenance and spending about 80% of each day resting on the sea ice.

To a large extent, the difference between the predicted and my estimated FMR may be a function of the emperor penguin's adaptation to winter reproduction. A more relevant comparison is that between the FMRs of the females in winter and those of the males venturing to sea in August following the chick changeover shortly after hatching. In late winter 1988, males breaking their winter fast consumed about 1.5 times the food and twice the metabolisable energy per day (89 g/kg and 440 kJ/kg, respectively, Robertson and Newgrain 1996) consumed by the females during the 1993 winter. Differences of this order would be expected, considering that the males were feeding after a four month fast and could spend almost twice as long each day foraging than the females.

Predictions of annual consumption rates of marine resources by antarctic predators (e.g. Woehler 1995) may be inaccurate because they lack data collected in winter. The present study demonstrates that emperor penguins consume less prey per day in winter than at other times of the year (see Robertson and Newgrain 1996). The lower consumption rates by emperor penguins in winter signal a potential error in predictions of annual prey requirements based on data collected in summer (e.g. Nagy 1987), when most antarctic seabirds and mammals breed. All penguin species require daylight to forage and must adapt to the reduced foraging time in winter. But unlike the emperor, other penguin species breed in spring and early summer; in autumn and winter, they forage for self-maintenance, which reduces their energetic demand at these times. For species that hunt at night, such as antarctic fur-seals (*Arctocephalus gazella*; Kooyman et al. 1986), consumption rates in winter may be higher than in summer because the long winter nights provide them with more opportunity to forage. Crabeater Seals apparently switch from predominantly nighttime foraging in summer to predominantly daytime foraging in winter, perhaps reflecting changes in prey or prey behaviour (Nordøy et al. 1995). Consumption rate estimates are a valuable tool for marine resource managers who provide quotas for fisheries that could compete with marine predators. There is a need for more studies assessing seasonal changes in the foraging ecology of marine predators to improve the accuracy of prey consumption rate estimates.

4.4.2 Role of winter foraging in the emperor penguin's breeding strategy

Emperor penguins are well adapted to their extraordinary winter breeding strategy. Female emperors arrive at the colony prior to courtship weighing 28.4 kg (Prévost 1961), fast for two months during courtship, lay a single 450 g egg (Mougin 1966), and return to sea having lost 20–25% of their body mass (Prévost 1961). By contrast, male emperors arrive at the colony with greater body masses (36.7 kg, Prévost 1961). Unlike other male birds, emperors are not territorial and do not expend energy on the establishment and maintenance of their territories (Montevecchi and Porter 1980), and have lost only a few kilograms of body mass when they commence the incubation.

Egg care solely by males is rare in birds; among penguins it is unique to the emperor (Oring 1982). In the king penguin (the emperor penguin's closest relative) males take the first incubation shift which lasts 30 days (55% of the incubation period), before being relieved by the females, who then stay with the eggs until hatching (Stonehouse 1960). King penguins may represent an intermediate evolutionary stage toward cold adaptation (Le Maho 1977), with the emperor penguin being the furthest evolutionary stage (Jouventin 1971). The evolution from the double-shift to the single-shift incubation strategy involves an increased fasting capacity for the male. However, rather than being instigated by the males wishing to retain the eggs for longer, this shift in incubation strategy was probably motivated by a decrease in the capacity of females to return to the colony during the incubation period. Perhaps, in the evolutionary history of emperor penguins, foraging in winter was particularly arduous, and the females had difficulty accumulating sufficient energy reserves to sustain a long fast. The present study has found conflicting evidence as to the ease or difficulty of foraging in winter. The findings that the females probably foraged close to the colony, took rest days, and gained 25% in body mass suggest that winter foraging may not be too stressful. However, the short day-lengths of winter and the extent of fast ice separating the colony from the feeding grounds may be critical factors preventing the females from returning to the colonies to relieve the males during incubation. Short day-lengths not only reduce the females' foraging time but also potentially increase the time it takes to commute to the colony across the sea ice (up to 8 days to travel one way). The females travelled mainly in daytime, as indicated by the regularity of nighttime huddles during commutes. I therefore support a speculation by Skutch (1957) that the energetic cost of crossing the expanse of sea ice that separates feeding grounds from the colony is a determining factor in the emperor penguins' single incubation shift.

A further consideration in the change from a double- to a single-shift incubation strategy is the potential for disruption to huddling males during a mid-incubation change. The period of arrival of females at the end of incubation lasts three to four weeks, and mate-finding causes considerable disruption to huddling males. If there were a mid-incubation changeover, the continual disruption would reduce the thermoregulatory advantage of huddling and would accelerate the depletion of the birds' fat reserves at a time of year when these reserves are difficult to recoup.

A final thought on the emperor's incubation strategy is that prey availability apparently varies between years. In many years, females may have difficulty gaining 25% of their body mass during winter foraging. Further study is necessary on the energy cost of diving, the role of rest periods, the role of huddling by females in energy conservation, and the distribution and abundance of prey in adjacent waters to more fully understand the environmental constraints on female emperor penguins in winter.

Appendix 4A. Regression equations for regular emperor penguin prey.

(i) Fish size from otolith length (OL) and jaw length (JL).

Species	Standard length (mm)	Mass (g)
[a,b]*Pleuragramma antarcticum*	$76.68 \cdot OL + 17.05$ $6.94 \cdot JL - 3.67$	$2.71 \times 10^{-6} \cdot SL^{3.2}$
[a]*Pagothenia borchgrevinki*	$96.50 \cdot OL - 84.26$	$5.62 \times 10^{-6} \cdot SL^{3.2}$
[a]*Trematomus eulepidotus*	$41.94 \cdot OL + 36.66$	$9.03 \times 10^{-7} \cdot SL^{3.6}$
[a,b]*Notolepis coatsi*	$14.35 \cdot OL + 87.06$ $7.33 \cdot JL - 7.52$	$2.19 \times 10^{-5} \cdot SL^{2.3}$
[a]*Electrona antarctica*	$42.70 \cdot OL + 0.28$	$9.53 \times 10^{-6} \cdot SL^{3.1}$

[a] after Williams and McEldowney 1990

[b] after R. Williams (unpublished data)

(ii). Squid size from lower rostral length (LRL) of beaks.

Species	Mantle Length (mm)	Mass (g)
[a]*Psychroteuthis glacialis*	$19.89 \cdot LRL + 58.84$	$10^{(1.61 \times \mathit{log}LRL + .80)}$
[b]*Alluroteuthis antarcticus*	$30.60 \cdot LRL$	$e^{(3.0 \times \mathit{ln}LRL + 1.14)}$
[c]*Kondakovia longimana*	37.32.LRL - 22.35	e(3.0 x lnLRL + 1.14)

a after Lu and Williams 1994

[b] after Rodhouse et al. 1990

[c] after Adams 1990

Appendix 4B

Foraging statistics of female emperor penguins from Auster and Taylor Glacier Colonies in the 1993 winter. Between-colony comparisons are made using unpaired t-tests.

Behaviour Parameter	Unit	Auster Colony				Taylor Glacier Colony				*t*-tests			Both colonies		
		n	Mean	±SD	Range	*n*	Mean	±SD	Range	df	*t*	*p*	*n*	Mean	±SD
Departing the colony															
Body mass	kg	25	25.4	*(1.9)*	22.2-29.4	6	25.2	(1.4)	24.2-27.8	29	0.25	0.81	31	25.4	*(1.8)*
Body-water pools	mL/kg	25	601.6	*(38.7)*	583.5-739.1	6	525.0	(31.1)	467.7-548.5	29	4.26	<.01^a	31	586.8	*(48.0)*
Winter foraging															
Trip duration	d	10	78.6	*(3.6)*	73-83	4	70.8	(3.0)	67-74	12	3.82	0.00a	14	76.4	*(5.0)*
^{b}Trip duration(TDR only)	d	4	78.5	*(3.1)*	76-83	4	70.8	(3.0)	67-74	6	3.60	0.01a	8	74.6	*(5.0)*
^{c}Rest days while at sea	% of d	10	8.5	*(7.4)*	0-23	4	2.6	(3.0)	0-6	12	1.52	0.15	14	6.8	*(6.9)*
Time in the water/day	h	10	4.8	*(0.3)*	4.4-5.3	4	5.4	(0.9)	4.8-6.7	12	2.01	0.07	14	5.0	*(0.6)*
Time/day – withoutT5	h	10	4.8	*(0.3)*	4.4-5.3	3	5.0	(0.2)	4.7-5.2	11	0.94	0.37	13	4.8	*(0.3)*
Dives per day	*n*	10	62.2	*(14.9)*	42.2-94.6	4	62.7	(18.4)	44.6-88.3	12	0.06	0.95	14	62.3	*(12.4)*
Feeding dives/day	*n*	10	25.3	*(6.7)*	19.2-38.9	4	26.9	(10.8)	16.2-41.7	12	0.51	0.62	14	25.9	*(7.7)*
Feeding dives/hour	*n*	10	5.8	*(1.4)*	4.2-8.3	4	4.9	(1.4)	3.1-6.4	12	1.15	0.27	14	5.6	*(1.4)*
Flat-bottom feed dive depth	m	10	162.1	*(23.3)*	128-214	4	265.5	(55.9)	199-318)	12	5.06	<.01a	14	191.6	*(58.7)*
Max. feeding dive depth	m	10	335	*(35.7)*	267-375	4	407	(70.3)	309-477	12	2.60	0.02a	14	355.1	*(56.3)*
Mean feeding dive duration	min	10	3.4	*(0.2)*	301-3.6	4	4.0	(0.7)	3.4-5.0	12	2.37	0.04a	14	3.6	*(0.5)*
DFeed div dur-without T6	min	10	3.4	*(0.2)*	3.1-3.6	3	3.6	(0.2)	3.4-3.8	11	1.59	0.14	13	3.5	*(0.2)*
Max dur of feed dive	min	10	12.0	*(1.8)*	9.4-15.2	4	11.8	(2.5)	8.8-13.8	12	0.21	0.84	14	12.0	*(1.9)*
Bottom time per feed dive	min	10	1.2	*(<0.1)*	1.0-1.3	4	1.3	(0.2)	1.1-1.6	12	1.57	0.14	14	1.2	*(0.1)*
^{d}Bottom time–without T6	min	10	1.2	*(<0.1)*	1.0-1.3	3	1.2	(<0.1)	1.1-1.2	11	0.23	0.82	13	1.2	*(<0.1)*

^{a}Denotes statistically significant differences at the $p<0.05$ level.

^{b}Trip durations are presented for all penguins combined and for only penguins that carried time-depth recorders (TDRs), to negate biases caused by transporting devices.

^{c}Percentages of rest days were arcsiue-transformed to homogenise variances.

^{d}Penguins T5 and T6 were separated from comparisons when their behaviours caused variances between the samples to differ significantly.

Appendix 4C

Comparisons between penguins that carried the larger satellite tracking devices (PTTs) or time-depth-speed recorders (Paddles) and penguins that carried the smaller time-depth recorders (TDRs) or were un-instrumented, to demonstrate the effects of the larger instruments on the penguins foraging.

Behaviour	Parameter	Unit	Penguins with PTTs or Paddles (n = 3)			Penguins with TDRs or no instrument (n = 5)			t test		
			Mean	±SD	Range	Mean	±SD	Range	df	t	p
Departing with the colony											
	Body mass	kg	52.6	(2.3)	23.4-28.0	25.7	(1.4)	24.0-27.8	6	0.06	.950
	Body-water pools	mL/kg	590.1	(22.9)	566.0-611.6	538.9	(45.1)	467.7-591.0	6	1.79	.123
Winter foraging											
	Foraging days	d	64.0	(1.0)	63-65	58.0	(3.0)	54-60	6	3.97	.004[a]
	Water intake/foraging day	mL/kg	47.4	(1.9)	45.9-49.5	55.0	(5.0)	48.5-60.1	6	2.48	.024[a]
	Prey consumed/for day	kg	1.5	(0.2)	1.4-1.7	1.8	(0.2)	1.7-2.0	6	2.93	.013[a]
	Pre consumed/for trip	kg	91.3	(4.5)	87-96	107.0	(7.0)	101-119	6	3.43	.014[a]
	Metabolisable energy intake	kJ/kg.d^{-1}	203.4	(8.1)	197.1-212.5	237.3	(21.2)	209.8-260.0	6	2.59	.041[a]
Returning to the colony											
	Body mass	kg	28.2	(1.8)	26.5-30.0	31.8	(2.4)	30.0-36.0	6	2.26	.066
	Mass gain while away	kg	2.6	(0.6)	2.0-3.1	6.1	(1.2)	5.4-8.2	6	4.85	.001[a]
	Trip duration	d	82.0	(1.0)	81-83	73.0	(4.0)	67-78	6	3.83	.004[a]

[a] Denotes stastically significant differences at the p<0.05 level.

5. SEASONAL CHANGE IN THE FORAGING ECOLOGY OF EMPEROR PENGUINS

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5.1 Introduction

Human fisheries in antarctic waters compete with wild predators for the same prey (Croxall et al. 1984, Ichii et al. 1996), and there is the potential in future for fisheries pressure to increase (Nicol and de la Mare 1993). To minimise the impact of the fisheries on the predator populations requires both a diligent management regime and an understanding of the trophic relationships between antarctic species, which may be highly variable. A major source of variability in trophic relationships in antarctic waters is the extreme contrast in conditions between summer and winter. During summer the sun remains up for several weeks and the sea ice around coastal areas reaches its minimum extent, whereas during winter the sun lies below the horizon for several weeks and a 1 m thick cover of fast ice covers the sea surface for up to 100 km from the coast (Zwally et al. 1983). The foraging strategies of antarctic marine species are intrinsically linked to this seasonality in solar influence and sea-ice cover. It is important to assess seasonal variations in the trophic relationships of antarctic species to develop management strategies designed to ensure the conservation of the antarctic ecosystem.

Antarctic seabirds are abundant predators in antarctic waters (Croxall 1984). Generally, the seabirds raise their young through spring and fledge them in summer when the foraging conditions for the fledglings are presumably most amenable. Conforming with this pattern is the largest seabird, the emperor penguin (*Aptenodytes forsteri*). These penguins have the longest chick raising period of any antarctic seabird (5 months) and must hatch their chicks in July (winter) in order to fledge them in early December (early summer) (Prévost 1954). This lengthy chick rearing period, which follows a four month courtship and incubation period, binds adult emperor penguins to the vicinity of the colonies for much of the year, and requires them to catch sufficient prey for themselves and their chicks between mid-winter and early summer.

Our knowledge of emperor penguin foraging ecology comes principally from single-season studies that have concentrated on a few aspects of the penguins' foraging ecology. Studies have assessed the birds' diving behaviour (Kooyman et al. 1971, 1992, Kooyman and Kooyman 1995), diet (Gales et al. 1990, Robertson et al. 1994a, Pütz 1995, and references therein), feeding rates (Robertson and Newgrain 1996), and foraging locations (Ancel et al. 1992). Despite this body of work, no studies have examined a range of aspects of the birds foraging ecology in the context of the seasonally fluctuating environment in which the emperor penguins must forage. In Chapter 4, I assessed the foraging ecology of female emperors in winter, which precedes the period of chick rearing. In this chapter, I report on seasonal changes in the penguins' foraging ecology during the five month period of chick care.

5.2 Methods

5.2.1 General

The study was undertaken at Auster colony (67°23'S, 64°04'E) and Taylor Glacier colony (67°28'S, 60°54'E) which lie 150 km apart on the Mawson Coast of Antarctica (Figure 5.1). In 1993, Auster colony contained 13 300 breeding pairs of emperor penguins and Taylor Glacier had 2 400 breeding pairs (Chapter 2).

Field work was conducted from the time of chick hatching until about one week before fledging (i.e. July to December), my stay being curtailed by deteriorating sea ice. For most experiments, penguins were selected randomly from the stream of individuals either departing from or returning to the colony. The exception was in July and August when birds departing the colonies were males that were in a weakened condition after their extended winter fast and I selected robust-looking individuals to carry instruments, to improve my chances of recovering the devices. Specific techniques employed in the study are described in Chapter 4 and are briefly outlined in the following sections. All birds were weighed to ± 0.1 kg and marked on the chest with 'Nyanzol' dye.

5.2.2 Determining foraging locations

To determine the foraging locations of male emperors departing Auster in July, I fitted three birds with satellite packs (PTTs; Model ST 6, Telonics Pty Ltd, USA) and tracked their movements. To reduce drag, each PTT was contained within a streamlined housing and had a trailing antenna. The PTTs were attached by hose clamps and 'Loctite 401' adhesive to feathers on the lower half of the birds' backs. Each PTT weighed 450 g and had a frontal surface area of 14 cm^2 (2.4% of the cross-sectional area of an average adult). The penguins' foraging locations after August were not investigated with PTTs, although clues to the foraging grounds were inferred from the availability of open water and its proximity to the colonies (deduced from satellite images), and known prey distributions.

5.2.3 Foraging behaviour

The foraging behaviours of penguins from Auster were sampled with time-depth recorders (TDRs, Model Mk 5, Wildlife Computers, USA); these were placed in streamlined housings and attached to the penguins' backs in a similar fashion to the PTTs. The combined mass of a TDR, its housing and the hose clamps was 100 g and the units had frontal surface areas of 4 cm^2 (<1% of the penguins' cross-sectional area). TDRs were deployed on 14 males leaving the colony in July and August when chicks were newly hatched, 14 birds in September when chicks were crèche age, and 10 birds in October, about mid-way through the chick growth period. Robertson (1994) found that up to 90% of birds fitted with instruments late in chick rearing abandoned the colony, so to minimise device loss and posible harm to the penguins in the present study, TDRs were not deployed after October.

Males departing in July and August were expected to forage for approximately three weeks, whereas in September and October, I anticipated trip durations of <20 days (Robertson and Newgrain 1996). To collect dive data for the entire trip periods, I staggered the start-up dates of the TDRs in July, August and

September. I found this was unnecessary for the shorter September trips, so in October I programed the TDRs to start sampling when deployed. The TDRs recorded depths >6 m at time intervals of 1, 2 or 5 sec (usually 2 sec). Generally, the TDRs sampled diving behaviour from single foraging trips, but occasionally data were obtained from the same bird on consecutive trips to sea.

The dive data were processed with software provided by the manufacturer of the TDRs (zero-offset-correction and dive analysis software). Dives to maximum depths of <10 m were ignored due to drift in the accuracy of the TDRs' pressure sensors (see Chapter 4). Dives to depths >10 m were categorised by visually assigning their profiles into non-foraging or foraging dives. During non-foraging dives, the penguins descended then ascended smoothly in short (<30 sec duration), shallow (usually to <20 m but occasionally to 50 m depth) profiles that were often performed in a series. The penguins presumably performed these dives when commuting through the water between foraging sites or recovering from feeding dives, or for social and self-maintenance purposes (e.g. grooming).

Foraging dives were defined as either search dives or feeding dives. Search dives (or perhaps navigation dives) appeared similar in profile to the non-foraging dives but were longer (0.5–8.0 min duration), deeper (50–400 m depth) and typically singular. Because there were no irregularities in the smooth descents and ascents of search dives to indicate prey were caught, these dives were not included in the analysis of feeding depths. Feeding dives were performed to any depth; the penguins descended then performed either a period of depth fluctuations (possibly indicating prey pursuit) or remained at one depth (perhaps indicative of benthic foraging) and then ascended to the surface. On shallow feeding dives, depth fluctuations indicative of prey pursuit were often performed during the ascent. The diving behaviours of penguins foraging concurrently, and the diving patterns of penguins foraging during different months, were compared.

5.2.4 Dietary composition

The diets of Auster and Taylor Glacier penguins were sampled on seven and two occasions respectively, by stomach-flushing birds (Wilson 1984) as they returned to their colony. A total of 121 penguins had their stomachs flushed; 94 from Auster and 27 from Taylor Glacier, with a minimum of 12 penguins flushed on each sampling occasion. The flushing procedure for each penguin was repeated until clear water was expelled, usually after 2–3 flushes. To ensure the stomach had been emptied, I also manipulated the penguins' abdomen by hand. The stomach contents were drained in a 0.5 mm sieve to remove excess water and stored frozen for later analysis.

In the laboratory, the stomach content samples were defrosted and re-drained by lightly pressing them by hand into a 5 mm sieve. This gave all the samples a similar degree of wetness. Each sample was weighed to ± 0.1 g (wet weight) and a representative 300 g subsample was extracted. Each subsample was placed in a plastic dish, then irrigated and panned up to 20 times to expose fish otoliths and jaws, squid beaks, and crustacean eyes. The number of fish otoliths in each subsample, divided by two, gave an estimate of fish numbers; counts of non-eroded lower beaks plus unpaired, but non-eroded, upper beaks provided an estimate of the squid numbers; the number of crustacean eyes divided by two gave an estimate of crustacean numbers. Fish masses were estimated from equations that correlated fish otolith or jaw lengths to fish mass (Williams and McEldowney 1990, R. Williams unpublished data, see Appendix 4A). When possible, fish sizes were estimated from jaws rather than otoliths, since otoliths of different sizes erode at different rates (Jobling and Brieby 1986, Van Heezik and Seddon 1989). Squid masses were predicted from lower-rostral-beak lengths (Clarke 1986, Adams 1990, Rodhouse et al. 1990, Lu and Williams 1994, see Appendix 4A). Euphausiids were too digested to measure so I assumed the mass of each *Euphausia superba* (Antarctic krill) and *E. crystallorophias* to be 0.60 g and 0.11 g respectively, these being the mean masses of individuals (excluding gravid females) caught during trawling on the Mawson Coast in January 1993 (G. Hosie pers. comm.). Amphipods and decapods were minor components and were sufficiently intact to weigh directly. A quantitative measure of the diet composition was obtained by combining the masses of the various prey that were represented in the 300g subsamples.

To develop the comparative quantification of the different prey types, I made several assumptions about their relative digestion rates in the penguins' stomachs. Previous researchers (e.g. Klages 1989), when assessing the diets of emperor penguins immediately after foraging, estimated fish, squid, and krill numbers from only pristine otoliths, beaks, and eyeballs, respectively. In the present study, I sampled from penguins that had fasted for 2–8 days while walking across the fast ice to the colony. Although the penguins might have delayed digestion to retain food to feed their chicks (Wilson et al. 1989b), there was probably some digestion/erosion of recognisable prey fragments during the penguin's journey. All recognisable otoliths were included because to count only pristine otoliths, which are composed of calcium carbonate and dissolve rapidly in seabird stomachs (Duffy and Laurenson 1983), may have underestimated the contribution of fish to the penguins' diet. Squid beaks are chitinous and may remain in an almost pristine condition in a penguin's stomach for several weeks (Pütz 1995); hence I considered only pristine beaks in this quantification of the squid proportion of the diet. Although krill eyes are also largely chitinous, the radules that comprise the outer surface of the eyes are bound together by proteins that may digest rapidly (G. Hosie, pers. comm.). Moreover, the eyes are soft inside and may readily burst in the penguins' stomachs; intact eyes were rarely sighted in the samples. I therefore counted all krill eyes to quantify the krills' contribution to the diet mix. In summary, the estimates of prey composition assumed all recognisable otoliths, non-eroded squid beaks, and all krill eyes remained in the penguins' stomachs for a similar period.

5.2.5 Estimating prey consumption rates

The prey consumption rates of between 20 and 23 penguins were estimated on five occasions, based on the turnover rates of tritiated water [^3H_2O] and equation [4] of Nagy and Costa (1980). Departing penguins were injected intramuscularly with 1 mL of distilled water containing 30 or 40 mCi of tritium (HTO), bled (2 mL from the radial vein) after a two hour isotope equilibration period, and released. When each tritiated penguin returned to the colony it was caught and re-bled. All blood samples were stored frozen and returned to the laboratory where aliquots of water were extracted by vacuum sublimation (Vaughan and Boling 1961) and assayed for radioactivity in a liquid scintillation counter. The penguins' body-water pools were estimated from levels of HTO in the blood prior to foraging. Rates of water intake during foraging were estimated from the dilution of the HTO between the pre- and post-foraging samples. Water intake rates were increased by 7% to compensate for the degree by which the HTO technique underestimates dietary water consumption (Chapter 3) and decreased by 2.4 mL/kg of body mass per day to account for incidental seawater intake (Robertson and Newgrain 1992). Emperor penguins occasionally eat snow at the colony (pers. obs.) and may do so at the ice-edge, but I have no measure of the quantities consumed. Therefore, in initial calculations of prey consumption rates, I provided for a hypothetical intake of 100 mL of water per day consumed as snow, which is probably excessive given the aerated nature of snow eaten by penguins and the volume necessary to yield the hypothetical amount. The 100 mL/d hypothetical value decreased the estimated rates of prey consumption by just 0.2 kg/d (<5%). Considering the large volumes of snow required to dramatically alter the prey consumption estimates, and my inability to accurately quantify the snow intake, I ignored snow consumption in the calculations of prey consumption. Because the birds gained mass while away, and because water stored during the isotope integration period is not labelled with HTO, the estimated nonlabelled water was subtracted from the total water intake for each penguin. To do this, I assumed that each penguin's mass gain (mass change minus mass of stomach contents) was fat and that fat yields 1.07 mL of water per g when metabolised (Schmidt-Nielsen 1975).

The penguins' water intake rates were converted to prey consumption rates by dividing water intake by the mean water content of the prey in the birds' diet mix. For this calculation, I assumed the total water (free plus metabolic) in fish, squid and crustacea was 0.85, 0.88 and 0.87 mL/g, respectively (Chapter 4). The penguins' metabolisable energy intakes were estimated from their prey consumption rates, incorporating the energy density of their diet (determined from bomb calorimetry of the stomach contents) and the efficiency by which emperor penguins assimilate energy from fish, squid and krill (81.8%,76.2% and 70.5% respectively; Robertson and Newgrain 1992, Chapter 3).

Unlike other penguin species that may enter the water and feed as soon as they leave the colony, emperor penguins raising chicks must travel over the sea ice for several days before reaching open water. To assess prey consumption and metabolic rates per foraging day, the number of over-ice travel days was subtracted from the number of days spent away from the colony. The travel days were recorded by the TDRs deployed between August and October, but after October, when TDR deployments ceased, the non-foraging days were estimated. These estimates took into account the overall trip durations, changes in the sea ice conditions, increasing day-length and escalating food requirements of the chicks, all of which presumably stimulated faster rates of travel by parents. Finally, while commuting the penguins would have metabolised body tissue, released water and diluted the HTO in body-water pools. The amount of water released was estimated by assuming the net specific cost of transport by a 23–30 kg emperor penguin was 17.5 J/kg·m^{-1} (Dewasmes et al. 1980) and by determining the distance travelled to and from the ice-edge from satellite images of the Mawson Coast. The estimated metabolic water released was subtracted from each penguin's total water intake prior to the calculation of prey consumption per foraging day.

5.2.6 Foraging trip durations

In July and August 25 female and 32 male penguins at Auster and six female and 24 male penguins at Taylor Glacier were fitted with VHF transmitters (80 g mass, 0.6% of the penguin's frontal area).

The attendance times and foraging trip durations of these penguins were monitored by scanning radio receivers that were connected to data loggers (Advanced Telemetry Systems, Minnesota, USA), powered by solar panels, and deployed at each colony. The receivers scanned each transmitter frequency for two periods of ten seconds each, every four hours. The system operated at Auster between July and early December and at Taylor Glacier between mid-September and late November.

At Auster, to augment the attendance data from the receiver, I patrolled the colony on foot on a near-daily basis and recorded the attendance of any penguins bearing plumage dye. This included all the birds I handled in other experiments and all birds carrying the radio transmitters. The reliability of these checks as a means of recording the presence of a marked penguin varied through the year. In July and August, the penguins were brooding small chicks and often huddled, which made resightings difficult. This difficulty was counteracted to some extent by the longer attendance times of the adults at this time of year which provided more opportunities for resighting. Between September and early November the birds were dispersed and remained at the colony for several days on each visit. Over this period it would probably have been rare for a marked bird to have passed through the colony without being sighted. In late November and early December many penguins visited the colony for less than a day (taking as few as four hours in one instance to find a chick, feed it and leave). I often patrolled the colony twice per day at this time, but birds may still have entered and departed between the checks.

5.2.7 Analyses

Means are presented ± 1 standard deviation. The differences between the means of samples in series were tested with pairwise Bonferroni comparisons after either nested or un-nested analysis of variances (ANOVAs), and *F* ratio tests for homogeneity of the variances. Significance was tested to the 0.05 level. For ease of comparison between certain non-parametric data sets (e.g. frequency of dive durations, which had skewed distributions), means were calculated.

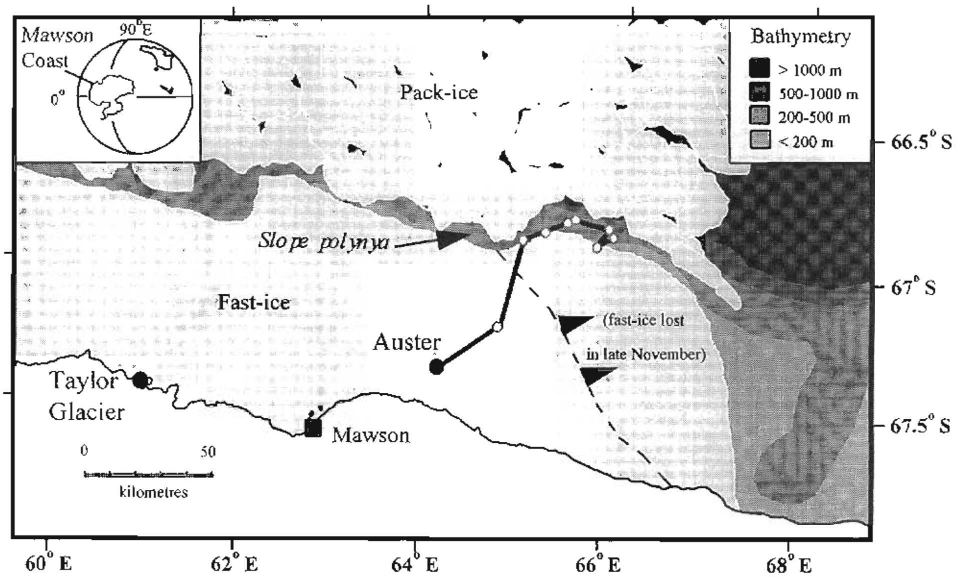


Figure 5.1 *Mawson coast showing the location of Auster and Taylor Glacier emperor penguin colonies, Mawson Station, bathymetry of the sea bed, sea ice conditions that prevailed between August and November 1993, and the path of a satellite tracked male penguin that departed Auster on 25 July. Dots on the penguin path represent 4 day intervals. The satellite pack failed on 27 August and the penguin returned to Auster on 8 September. In late November, a large section of the fast ice east of Auster blew away (indicated by dashed lines and arrows) exposing the continental shelf <50 km from the colony.*

5.3 Results

5.3.1 Body masses and mass gains

The mean body masses of emperors departing Auster increased from 22.9 ± 1.7 kg (n = 40 birds) in early September to 24.7 ± 1.3 kg (n = 20) in November (ANOVA: $F_{4,137} = 5.56$: $p < 0.001$). The male penguins leaving in August after their long winter fasts had body masses that averaged 23.5 ± 1.2 kg (n = 30). On return to the colony, these males had gained 4.1 ± 1.9 kg (n = 6 penguins). All birds in this sample carried TDRs which might have reduced their ability to gain mass. Uninstrumented penguins foraging later in the year gained 4.0 ± 1.7 kg (range -0.5 to +8.0 kg, n = 30). There was no indication of a decrease in mass gained per trip as the seasons progressed (ANOVA for uninstrumented birds: $F_{4,31} = 0.54$; $p = 0.71$) despite trip durations gradually decreasing (see below).

5.3.2 Foraging location

One PTT functioned for 64 days (72% of trip length) but the remaining two PTTs failed after 4–8 days. After departing Auster in late July the tracked penguin travelled in a north-easterly direction taking about 7 days to cross the 60 km

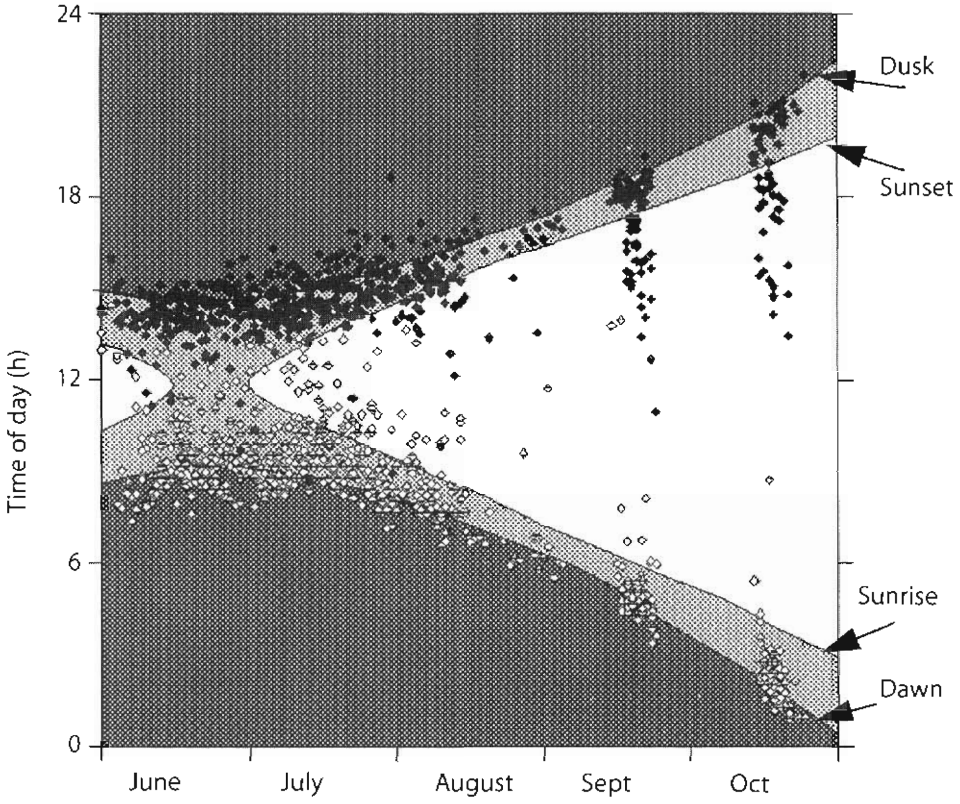


Figure 5.2 *Water entry (open diamonds) and water exit times (closed diamonds) of emperor penguins foraging along the Mawson Coast in 1993 (includes winter data from Chapter 4), as well as local dawn/dusk and sunrise/sunset times (UTC plus 4 hours, 67°S); dawn and dusk occured when the sun was 3° below the horizon.*

of fast ice to the ice-edge (Figure 5.1). At the time the ice-edge lay over the continental slope and was flanked by a 10–20 km wide polynya that separated the edge of the fast ice from pack ice regions to the north. The tracked bird foraged in this polynya for at least 25 days, when the PTT failed, then returned to the colony 13 days later.

The fast ice along the Mawson Coast remained stable until late November when large sections of ice east of Auster broke away (see Figure 5.1). This break-out reduced the distance the penguins had to travel to reach open water to <50 km.

5.3.3 Diving behaviour

All but one of the dive-recorders were recovered and data were retrieved for 13, 14 and 10 penguins foraging in August, September and October, respectively. The duration of travel between the colony and the ice-edge decreased from 3–10 days in July and August to 2–5 days in September and 2–3 days in October

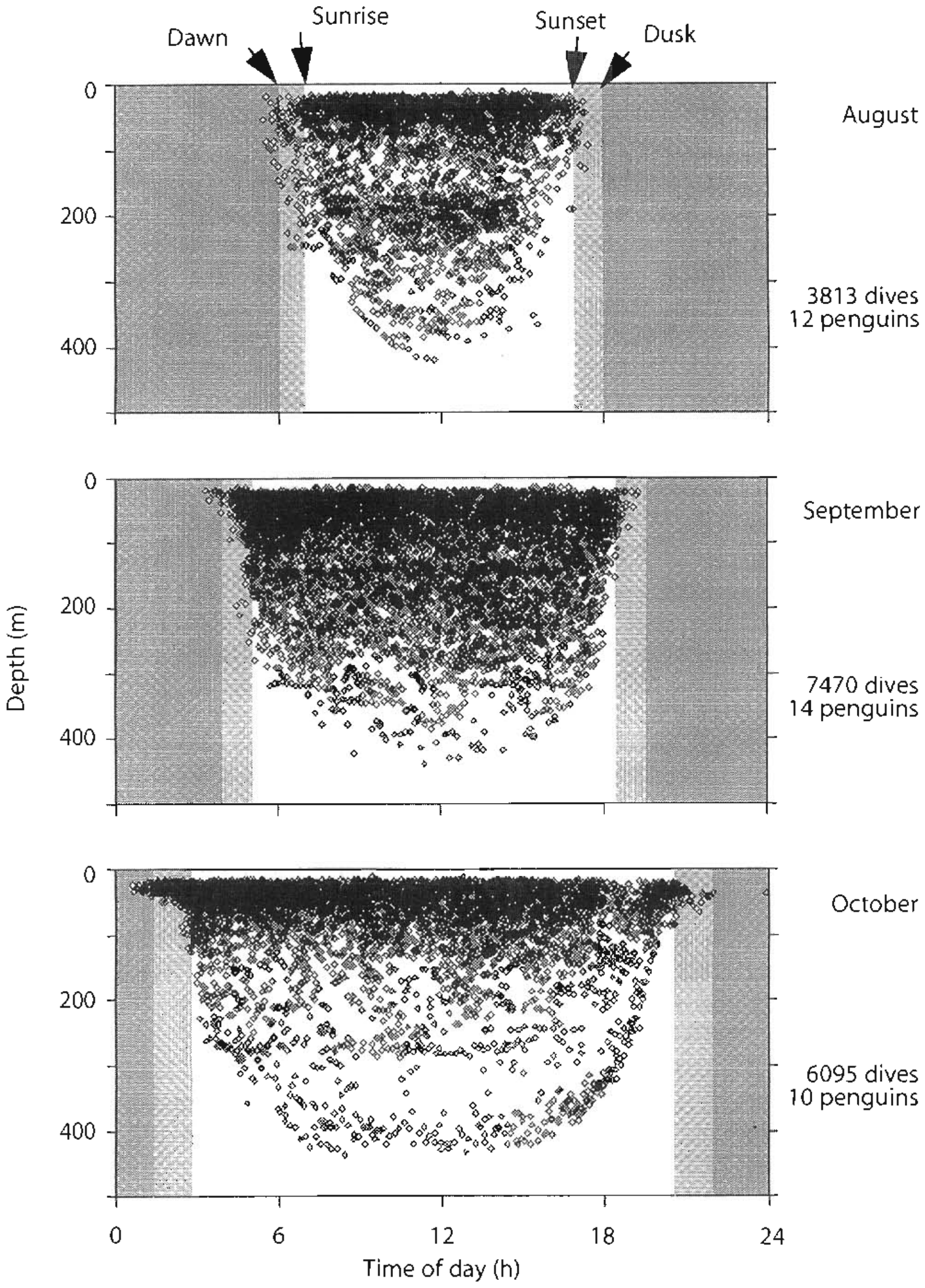


Figure 5.3 *Depth of feeding dives relative to time of day (local solar time) recorded for Auster penguins in August, September and October. Times of dawn, sunrise, sunset and dusk are for the longest day of each month. Darker shading represents nighttime, lighter shading represents twilight and no shading represents daytime.*

(Table 5.1). In all three periods the penguins averaged 10–12 days at sea (range 5–19 d) with the greatest variation between individuals occurring in September (12.0 ± 5.3 d). The TDRs recorded data for 90, 88 and 66 total days at sea for the three periods, respectively.

While at sea the penguins foraged daily, customarily entering the water around dawn and exiting at a range of times but mostly before dusk (Figure 5.2). No complete rest days were recorded although the birds took rest periods, remaining out of the water between bouts of swimming on 10.6%, 10.5% and 63.6% of days recorded during August, September and October respectively. Of the penguins carrying TDRs, 41%, 64% and 100% took rest periods during the three months, respectively. Usually one, but up to three, rest periods were taken in a single day with the mean duration of each rest period increasing between August and October from 1.6 ± 0.7 hours (n = 10 days, range 1–3 h) to 2.9 ± 2.1 hours (n = 61, range 0.5–10 h), although this increase was not statistically significant (ANOVA: $F_{2,82} = 2.95, p = 0.06$). Penguins taking rest periods late in the day and not re-entering the water before nightfall may account for the broad spread of water exit times in September and October (see Figure 5.2).

Despite the increased frequency of rest periods over time, the penguins' daily swimming time increased from 7.83 ± 1.50 hours in August, to 12.23 ± 1.25 hours in September, and 12.95 ± 1.24 hours in October (Table 5.1). The swim time, as a proportion of time at the ice-edge, rose from 32.7%, to 51.2% and 55.1%, respectively in these months (Table 5.1). Accordingly, the penguins' dive rate increased from 92.7 ± 28.5 dives/d, to 149.4 ± 23.4 dives/d, and 161.6 ± 19.3 dives/d, respectively. In addition, both the proportion of dives classed as feeding dives (56%, 61% and 62% respectively) and the hourly rate of feeding dives (6.5, 7.4 and 7.7 dives/h, respectively) increased over the same months (Table 5.1). As a result, the penguins' frequency of feeding dives increased from 51.7 ± 15.2 dives/d in August, to 90.5 ± 15.3 dives/d in September and 100.8 ± 12.6 dives/d in October, respectively.

Immediately after dawn the penguins foraged at shallow depths (typically <100 m, Figure 5.3). As the day progressed, however, the range of foraging depths increased, peaking around mid-day when depths >400 m were occasionally attained; dive depth then decreased toward evening.

During August and September the majority of birds foraged mainly at depths <100 m, although the feeding depths of individuals varied considerably. For example, in September one penguin hunted at depths between 100–200 m on 70% of its feeding dives and another penguin hunted prey deeper than 300 m on 31% of its dives. There was less individual variation in dive depth during October than in August or September with all but one of the birds targeting prey primarily between 20–50 m (37–59% of feeding dives). There was distinctly less feeding below 100 m depth in October (23% of dives) than there had been in August and September (44% and 46% of dives respectively; 37% of dives during the three months combined; Figure 5.3). Penguins for which dive records were obtained on consecutive foraging trips tended to reduce their frequency of dives to depths >100 m on their second trip.

The maximum dive depths and maximum dive durations achieved by the penguins did not vary significantly between months and averaged 330.2 ± 66.7 m and 9.48 ± 1.85 min, respectively (see Table 5.1). Mean foraging dive durations were significantly longer in September (4.31 ± 1.53 min) than August (3.87 ± 1.55 min) or October (3.70 ± 1.53 min; nested ANOVA: $F_{2,34} = 45.7$: $p < 0.001$) which probably reflected the frequent deep diving by some penguins in September and the fact that deep dives tended to last longer than shallow dives (Figure 5.3).

5.3.4 Dietary composition

The body masses of penguins stomach-flushed on their return from foraging trips were similar between sampling dates and averaged 29.2 ± 2.2 kg (ANOVA: $F_{8,118} = 0.92$, $p = 0.5$). The wet food mass in the birds' stomachs varied seasonally (ANOVA: $F_{8,112} = 4.94$, $p < 0.001$), being lowest at Taylor Glacier in September (0.9 ± 0.6 kg, $n = 15$) and highest at Auster in early October (2.0 ± 0.5 kg, $n = 12$; Table 5.2). On average, each penguin yielded 1.3 ± 0.6 kg of food ($n = 121$, range 0.3-2.5 kg). Gastric stones were recovered from 90% of penguins flushed.

Data on the relative proportions of prey types in the diet, water and energy contents of the prey and the predicted dietary assimilation efficiencies that were incorporated into the prey consumption calculations are shown in Table 5.2.

Recognisable fragments of fish, squid and crustacea were present in 96, 60 and 88%, respectively, of the Auster samples ($n = 94$) and in 93, 59 and 100% of the Taylor Glacier samples ($n = 27$). Of the 24 prey taxa identified to species 15 were fish, four were squid and five were crustaceans (Table 5.3).

The fish component of the penguins' diet on all sampling occasions was dominated numerically by antarctic silverfish (*Pleuragramma antarcticum*), although at times *Notolepis coatsi*, *Pagothenia borchgrevinki* or a *Trematomus* species contributed more to the diets by mass (Figure 5.4). A Myctophid, *Electrona antarctica*, was common in late October and early November samples from Auster, although its otoliths were highly eroded. Antarctic silverfish and *N. coatsi* were the only fish species present on all sampling occasions and the only fish species for which sufficient numbers of non-eroded jaws were obtained to assess seasonal changes in size. The sizes of the antarctic silverfish and *N. coatsi* taken, however, were small and remained relatively constant through the year, averaging 2.1 ± 1.4 g (66 ± 11 mm SL, $n = 367$) and 4.4 ± 2.1 g (178 ± 37 mm SL, $n = 171$), respectively (Figures 5.5a,b).

The glacier squid (*Psychroteuthis glacialis*) dominated the squid component of the birds' diet on all but two occasions, the exceptions being at Auster in September and early October when fewer but larger (up to 500 g body mass) *Alluroteuthis antarcticus* contributed a greater mass to the diet. Beaks from the large, oceanic squid *Kondakovia longimana* were encountered but always were very eroded; hence, I ignored them in the interpretation of prey composition, although *K. longimana* may be an important dietary component of emperor penguins when foraging a long way from their colonies. The penguins consumed two size classes of glacier squid; large (>140 mm) individuals were taken in

Table 5.1 *Foraging behaviour of emperor penguins as determined from time-depth recorders (TDRs).*

		Month									ANOVA			Total			
		August			September			October									
	Units	x	±SD	[a]*n*	x	±SD	[a]*n*	x	±SD	[a]*n*	df	F	P	x	±SD	*n*	range
Chick stage		brood			early-crèche			late-crèche									
Trip sections																	
Time to reach the ice-edge	d	8.4	*3.9*	5	2.5	*0.7*	8	2.1	*2.1*	9	2,19	20.70	<.001			22	1.7-11.8
Time at the ice edge	d	10.2	*2.4*	5	12.0	*5.3*	8	12.0	*3.0*	8	2,18	0.37	.69	12.0	*3.0*	21	5.0-19.0
Time to return to colony	d	6.0	*1.4*	2	4.5	*2.1*	4	3.0		1	2,4	0.86	.49	4.7	*1.9*	7	2.0-7.0
Diving behaviour																	
[b]Water entry time each day	h	7.3	*1.3*	12	4.7	*0.8*	14	2.4	*0.6*	10	**2,32**	**6.56**	**<.001**			36	1.7-8.6
[b]Water exit time each day	h	15.4	*0.8*	12	14.3	*0.8*	14	18.3	*1.2*	10	**2,32**	**1.16**	**.27**	16.9	*2.4*	36	13.9-20.5
[c]Penguins that took rest periods	%	41			64			100									
Days containing rest periods	%	10.6			10.5			63.6									
[d]Mean duration of rest periods	h	1.6	*0.7*	10	2.1	*1.3*	14	2.9	*2.1*	61	2,82	2.95	.06	2.6	*1.9*	83	0.5-10.0
[e]Time at ice-edge spent swimming	%	32.7	*5.9*	12	51.2	*4.7*	14	55.1	*5.3*	10	2,33	58.94	<.001			36	26.9-58.8
[b]Hours in water	d-1	7.83	*1.50*	12	12.23	*1.25*	14	12.95	*1.24*	10	**2,32**	**1.98**	**.003**			36	5.5-14.4
[b]Dive rate	d-1	92.7	*28.5*	12	149.4	*23.4*	14	161.6	*19.3*	10	**2,32**	**2.83**	**<.001**			36	49.1-186.2
	h-1	11.6	*1.6*	12	12.3	*1.8*	14	12.5	*1.6*	10	**2,32**	**2.49**	**<.001**			36	9.0-16.0
Feeding dives																	
[e]Proportion of all dives	%	56.1	*7.2*	12	61.0	*9.2*	14	62.0	*4.6*	10	2,33	2.08	.14	59.6	*7.7*	36	43.4-70.4
[b]Feeding dive rates	d-1	51.7	*15.2*	12	90.5	*15.3*	14	100.8	*12.6*	10	**2,32**	**2.21**	**.001**			36	31.1-125.5
	h-1	6.5	*1.0*		7.4	*1.0*		7.7	*1.0*		**2,33**	**1.96**	**.004**			36	5.3-9.6

		Month									ANOVA			Total			
		August			September			October									
	Units	$\bar{x}$	±SD	[a]*n*	$\bar{x}$	±SD	[a]*n*	$\bar{x}$	±SD	[a]*n*	df	F	P	$\bar{x}$	±SD	*n*	range
Depth ratio, 10-20:-50:-100:-200:-300:>300m	%	2:29:25:24:16:3		13	1:27:26:28:13:4		14	3:46:25:14:6:4		10				2:34:27:22:1:4		37	
Maximun depth	m	318.3	*71.7*	13	362.4	*56.1*	14	327.3	*69.9*	10	2,34	0.66	.52	330.2	*66.7*	37	183-438
Duration ratio,. 0-1.5: -3: -5: -8: >8min	%	2:2:45:24:1		13	1:21:47:30:1		14	3:33:46;16:1		10				2:27:46:23:1		37	
Maximum duration	min	8.9	*1.6*	13	9.9	*1.5*	14	9.7	*2.5*	10	2,34	1.15	.33	9.5	*1.9*	37	6.0-15.7

[a] *n* = number of penguins except for the mean duration of rest periods where *n* = number of rest periods.

[b] Nested ANOVAs (emboldened) performed on data series from penguins within months.

[c] Rest periods taken during daylight hours.

[d] Although data were not normally distributed, means are presented for convenience. ANOVAs were performed after ln (x + 1) transformation of data to homogenise the variances and scale zeros into the positive range.

[e] ANOVAs were performed after arcsine √ transformation of percentage data to homogenise the variances.

Table 5.2 *Mean wet mass of stomach contents flushed from emperor penguins returning to Auster and Glacier Colonies during 1993; prey components determined from the stomach contents as a percentage by mass, water and energy content of the prey and the calculated efficiency by which the penguins could assimilate the diet mix.*

Date	Colony	Mean mass of stomach contents (g)	Diet Mix (%)			[a]Water content (%)	[b]Energy content (kJ/g)	[c]Assimilation efficiency (%)
			Fish	Squid	Krill			
23 Aug.	Auster	1179.8	27.3	5.2	67.5	0.865	5.16	0.739
15 Sept.	Taylor	911.6	28.3	6.0	65.7	0.865	5.11	0.740
20 Sept.	Auster	1150.4	33.0	13.1	53.9	0.865	5.19	0.750
11 Oct.	Auster	1995.7	32.7	25.5	41.8	0.866	5.43	0.756
25 Oct.	Auster	1606.2	32.0	24.6	43.4	0.866	5.53	0.755
5 Nov.	Taylor	1336.3	10.9	58.3	30.8	0.874	5.19	0.751
11 Nov.	Auster	1185.8	14.5	48.7	36.7	0.871	5.37	0.748
25 Nov.	Auster	1373.7	24.4	64.2	11.4	0.872	5.48	0.769
3 Dec.	Auster	1278.8	74.8	24.5	0.7	0.857	5.41	0.803

[a] Free plus metabolic water content calculated assuming the water contents of the fish, squid and krill were 0.85, 0.88 and 0.87 mL/g, respectively (Chapter 4).

[b] Energy content determined by bomb calorimetry of stomach contents.

[c] Overall dietary assimilation efficiency calculated assuming the proportions 81.8%, 76.2% and 70.5% of fish, squid and krill respectively could be assimilated (Robertson & Newgrain 1992, Chapter 3).

***Table 5.3** Summary of results from the analysis of prey represented in 300-g sub-samples of emperor penguin stomach contents (n = 121) collected at Auster and Talor Glacier Colonies from August to December 1993.*

Prey species	Stomachs		^{a}Individual prey				^{d}%contribution	
	(*n*)	(%)	total (*n*)	^{b}non-erod. (*n*)	^{c}mass/ item(g)	^{d}total mass(g)	by number	by mass
Fish:								
Fam. Channychthydae								
Chaenodraco wilsoni	2	(2)	2	1	185.1	370.2	<0.1	0.8
Neopagetopsis ionah	2	(2)	3	0	24.9	74.4	<0.1	0.2
Pagetopsis macropterus	1	(1)	1	1	24.9	24.9	<0.1	0.1
Pagetopsis sp.	3	(2)	4	1	47.6	190.2	<0.1	0.4
unidentified channichthyid	11	(9)	19	0	32.0	607.2	0.1	1.3
Fam Gempylidae								
Paradiplospinus gracilis	1	(1)	1	0	14.9	14.9	<0.1	<0.1
Fam. Myctophidae								
electrona antarctico	13	(111)	132	0	6.9	914.8	0.3	1.9
krefftichthys anderssoni	3	(2)	5	0	6.9	34.7	<0.1	0.1
gymnscopelis braueri	1	(1)	1	0	6.9	6 9	<0.1	<0.1
Unidentified myctophid	1	(1)	44	0	6.9	27.7	<0 1	0 1
Fam. Nototheniidae								
Pleuragramma antarcticum	90	(74)	1516	57	2.0	3058.0	4.0	6.5
Pagothenia borchgrevinki	3	(2)	14	1	140.3	1964.4	<0.1	4.2
Trematomus bernachii	1	(1)	2	0	85.9	171.8	<0.1	0.4
T. enlepidotus	7	(6)	16	3	84.3	1348.0	<0.1	2.9
T. lepidorhinus	2	(2)	5	2	135.3	676.7	<0.1	1.4
T. loennbergi	1	(1)	1	0	127.3	127.3	<0.1	0.3
T newnesi	1	(1)	11	0	52.4	576.4	<0.1	1.2
Trematomus sp.	7	(6)	8	0	81.3	650.2	<0.1	1.4
unidentified notothenid	9	(7)	20	0	95.4	1907.8	0.1	4.0
Fam. Paralepidae								
Notolepis coatsi	35	(29)	143	9	5.5	788.3	0.4	1.7
unidentified fish	14	(12)	25	0	10.0	250.0	0.1	0.5
Total	115	(95)	1933	75	7.1	13785.1	5 1	29.2
Cephalopods:								
Psychroteuthis glacialis	63	(52)	674	351	17.9	12056.4	0.9	25.6
Alluroteuthis antarctieus	30	(25)	74	2	21.6	1595.3	<0.1	3.4
Kondakovia longimana	17	(14)	66	1	1.5	96.2	<0.1	0.2
Gonatus antarcticus	3	(2)	3	0	0	0	<0.1	<0.1
Bathoteuthis sp.	1	(1)	1	1	19 1	19.1	<0.1	<0.1
Total	72	(60)	818	375	19.8	13767.0	0.1	29.2

continued on page 97

Prey species	Stomachs		[a]Individual prey				[d]%contribution	
	(*n*)	(%)	total (*n*)	[b]non-erod. (*n*)	[c]mass/ item(g)	[d]total mass(g)	by number	by mass
Crustacea:								
Fam. Euphausiacea								
Euphausia superba	107	(88)	32052		0.6	19231.2	84.4	40.8
E. chystullorophias	1	(1)	3582		0.1	394.0	9.4	0.8
Fam. Amphipoda								
Hyperia macrocephala	7	(6)	12		0.1	1.2	<0.1	<0.1
Abyssorchomene rossi	6	(5)	10		0.1	1.0	<0.1	<0.1
Eusirus sp.	5	(4)	7		0.1	0.7	<0.1	<0.1
Fam. Decapoda								
Notocrangon antarcticus	2	(2)	2		0.8	1.6	<0.1	<0.1
Total	110	(91)	35662		0.6	19629.4	93.9	41.6
Total Overall	121	(100)	37970		1.2	47181.6		

[a] Fish represented by otolith pairs, squid by lower-rostral beaks and crustacea by pairs of eyes.

[b] Fish and squid represented by non-eroded otoliths and beaks respectively.

[c] See text for the source of individual prey masses

[d] Total mass of prey items and dietary contributions calculated from all fish, only non-eroded squid and all crustacea.

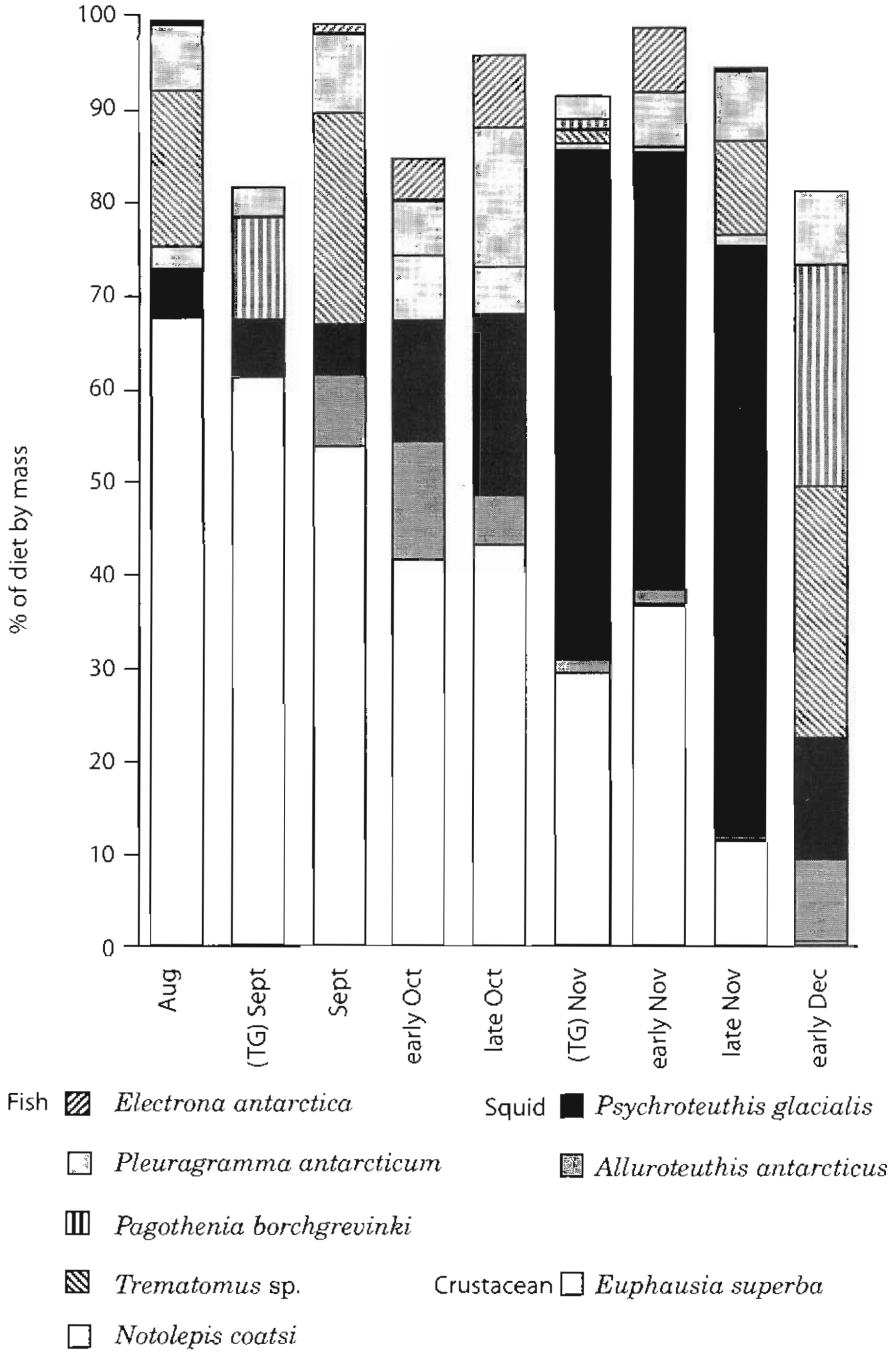


Figure 5.4 *Composition by mass of the main prey species in the diet of the emperor penguins on the Mawson Coast in 1993. Collections were made at Auster Colony in all months between August and December, and at the Taylor Glacier Colony (TG) in September and November.*

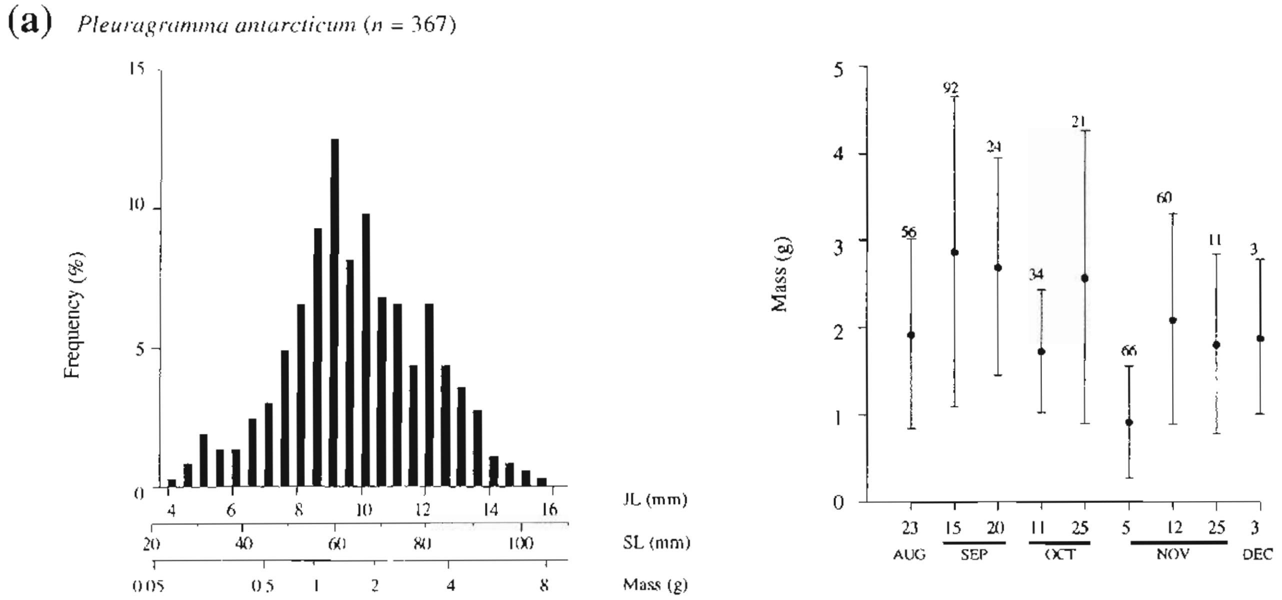
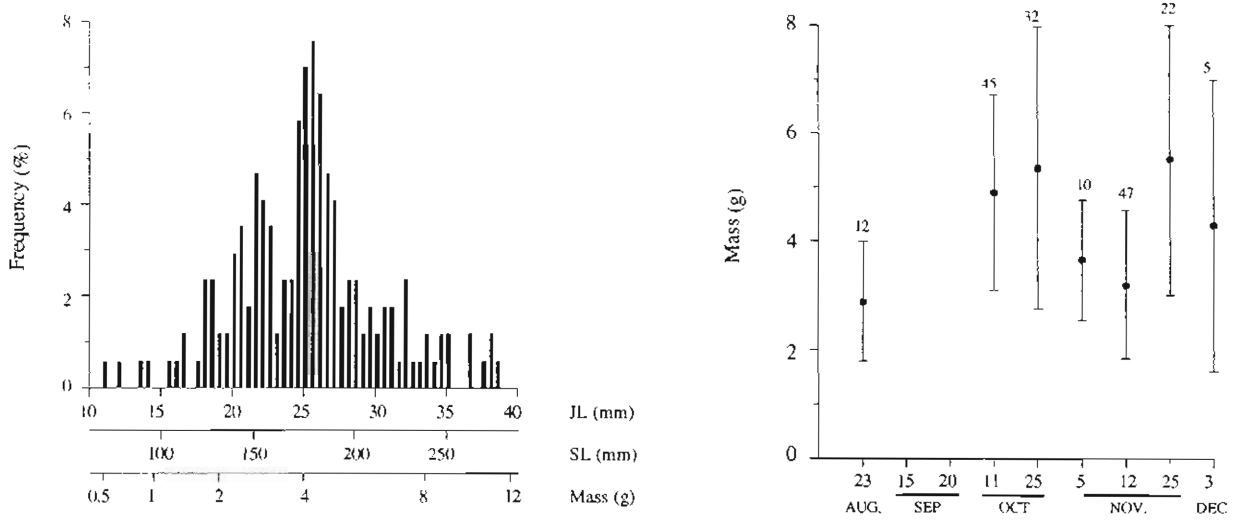


***Figure* 5.5** *Size frequency distribution and changes in mean (± SD) mass with time of* Pleuragramma antarcticum *(a),* Notolepis coatsi *(b) and* Psychroteuthis glacialis *(c) eaten by emperor penguins on the Mawson Coast in 1993. Note: the penguins ate* P. glaciais *from two distinct cohorts.*

Figure 5.5 (c) on page 100



(b) *Notolepis coatsi* (n = 171)

(c) *Psychroteuthis glacialis* (n = 350)

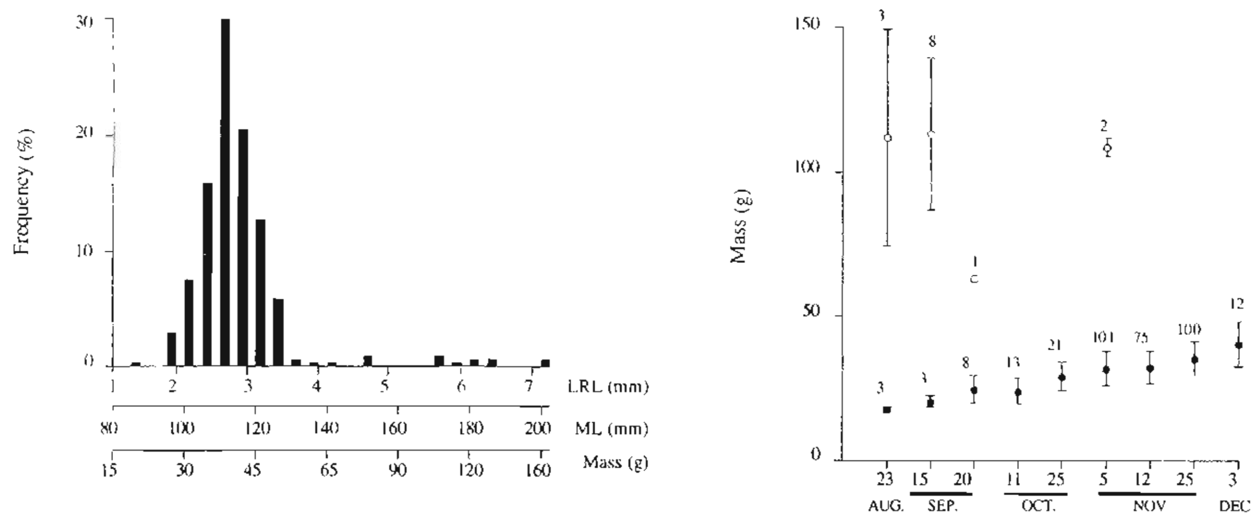


Figure 5.5 (c)

August and September but rarely thereafter when the penguins fed almost exclusively on small squid that increased in size between August and December from 17.8 ± 1.0 g mass (96.9 ± 1.2 mm mantle length, n = 3) to 40.6 ± 7.7 g (122.0 ± 7.6 mm, n = 9; Figure 5.5c). On most sampling occasions, over 50% of the penguins that were flushed had eaten small glacier squid. A total of 71 non-eroded beaks was extracted from a single 300 g subsample collected at Auster in late November.

Antarctic krill dominated the crustacean component of the penguins' diet, but in September one Taylor Glacier penguin yielded only *E. crystallorophias*, this being the only observation of this prey in the samples. Other crustacea consumed occasionally were the amphipods *Hyperia macrocephala*, *Abyssorchomene rossi* and *Eusirus* sp., and a decapod *Notocrangon antarcticus*.

Penguins at both colonies ate similar prey although Auster penguins tended to catch fewer crustaceans and more fish than did Taylor Glacier penguins. antarctic krill dominated the diets at both colonies: 92% by number and 37% by mass at Auster, and 74% by number and 52% by mass at Taylor Glacier. The relative importance of krill decreased through time from 68% of the diet by mass in August, to <1% in early December (Figure 5.4). Overall, glacier squid were the next most important dietary items by mass (26% at Auster and 25% at Taylor Glacier) and were eaten most frequently in November (47–63% at Auster and 57% at Taylor Glacier). Other prey species contributed to the diets either regularly, as did antarctic silverfish (7 ± 4% of the diet by mass; range 3–15%; n = 9 sampling times), or irregularly, as did various *Trematomus* species (9 ± 11%; range 0–27%), the *A. antarcticus* (4 ± 5%; range 0–13%) and *P. borchgrevinki* (4 ± 8%; range 0–24%).

5.3.5 Water intake and prey consumption rates

Male penguins departing Auster in July and August had significantly lower body-water pools than did penguins of both sexes departing later in the year (583.4 ± 31.7 mL/kg, n = 23 versus 645.0 ± 40.1 mL/kg, n = 83 respectively; ANOVA: $F_{4,101}$= 11.30: $p < 0.001$). The males were probably dehydrated after their long winter fasts. Water intake and prey consumption rates were determined only for penguins caught and bled before they re-entered the colony and fed their chicks, which reduced the sample sizes to 4, 18, 11, 12 and 9 penguins that foraged during August, September, October, early November and late November, respectively. The penguins' water intakes calculated per day away from the colony increased more than two-fold over the chick rearing period from 90.2 ± 9.4 mL/kg during August to 222.2 ± 34.7 mL/kg during late November (Table 5.4, Figure 5.6). These rates were equivalent to the consumption of 2.6 ± 0.2 kg and 6.8 ± 1.0 kg of prey per day away from the colony, respectively.

The consumption rates per day away from the colony were converted to rates per foraging day after accounting for commuting days based on the TDR data. During August, September and October the mean number of days it took penguins to travel to or from the ice-edge were 4, 3.5 and 2.5, respectively. I assumed the penguins took 2 days to travel to the ice-edge in early November

***Table 5.4** Mean water intake and prey consumption rates by emperor penguins from Auster Colony during foraging trips in different months (± 1 SD in parenthesis).*

Departure	Penguins	Mean	Mass	Per day away from colony				Prey	Per foraging day				
month		body mass	change	Days	[a]H_2O intake	[b]Prey consumed		[c]Metabolisable energy intake	consumed per trip	[d]days	H_2O intake	Prey consumed		Metabolisable energy intake
	(*n*)	(kg)	(kg)	(*n*)	(mL/kg)	(g/kg)	(kg)	(kJ/kg)	(kg)	(*n*)	(mL/kg)	(g/kg)	(kg)	(kJ/kg)
August	4	24.7	3.8	19	90.2	104.3	2.6	397.0	44	11	142.6	164.9	4.0	628.0
		(0.6)	*(0.6)*	*(4)*	*(9.4)*	*(10.9)*	*(0.2)*	*(41.5)*	*(10)*	*(1)*	*(30.4)*	*(35.2)*	*(1.0)*	*(133.9)*
September	18	24.6	4.0	20	121.3	140.2	3.4	545.0	65	13	189.2	218.8	5.4	850.4
		(2.1)	*(1.6)*	*(4)*	*(34.7)*	*(28.6)*	*(0.7)*	*(111.0)*	*(22)*	*(4)*	*(44.8)*	*(51.8)*	*(1.3)*	*(201.4)*
October	11	25.7	4.1	23	136.1	156.5	4.0	654.2	87	18	174.5	200.6	5.1	838.5
		(1.9)	*(1.9)*	*(5)*	*(27.7)*	*(31.8)*	*(0.8)*	*(133.0)*	*(20)*	*(5)*	*(42.9)*	*(49.3)*	*(1.2)*	*(206.2)*
early November	12	26.8	3.4	13	187.1	213.8	5.7	901.1	71	9	284.2	324.8	8.7	1368.9
		(1.4)	*(1.2)*	*(4)*	*(19.1)*	*(21.8)*	*(0.6)*	*(91.8)*	*(25)*	*(4)*	*(53.4)*	*(61.1)*	*(1.9)*	*(257.4)*
late November	9	26.5	4.2	9	222.2	257.2	6.8	1110.4	61	7	284.6	329.4	8.7	1422.0
		(2.2)	*(2.1)*	*(3)*	*(34.7)*	*(44.0)*	*(1.0)*	*(220.2)*	*(20)*	*(3)*	*(61.7)*	*(71.4)*	*(1.7)*	*(308.4)*

[a] Tritium-derived water intakes adjusted up 7% to account for inherent underestimate in the tritium technique (Chapter 4), we subtracted 2.4 mL/kg of body mass per day to account for sea-water injestion (Robertson & Newgrain 1992) and non-metabolised water accumulated in the body tissue (mass gain minus mass of stomach contents) assuming all mass gain was fat which could release 1.07 mL/g of water when metabolised.

[b] To determine daily prey consumption, water intake was multiplied by the water contents (free plus metabolic) of prey in the dietary mix (in Table 5.2).

[c] Metabolisable energy intake was calculated by multiplying mass-specific prey consumption rates by the mean assimilation efficiency by emperor penguins (Table 5.2).

[d] Foraging days equal days away minus days of travel over fast-ice (see text). For the calculation, we subtracted metabolic H_2O released during travel (see text) from the total water intake.

and 1 day to cover the distance in late November, when the loss of fast ice reduced the distance between the colony and the ice-edge from 80 km to 50 km. Due to the reduced travel times, metabolic water released during travel (which was subtracted from total water turnover) declined from 2 440 mL in August to 1 500 mL in late November. Taking into account the adjustments, the penguins' estimated prey consumption rates per foraging day doubled from 4.0 ± 1.0 kg/d during August to 8.7 ± 1.7 kg/d in late November (Table 5.4, Figure 5.6). These rates were equivalent to metabolisable energy intake rates of 628.0 ± 133.9 kJ/kg and 1422.0 ± 308.4 kJ/kg per foraging day, respectively.

5.3.6 Foraging trip durations

Data from the remote attendance receiver at Auster were incomplete because the colony expanded to several km^2 in spring and encircled grounded ice bergs which blocked the radio signals. Therefore, visual monitoring was relied on to obtain attendance records at this colony. Many of the birds that were marked and monitored apparently did not continue to raise chicks, perhaps in response to my manipulation or the death of their chicks. These birds either remained at the colony for long periods without attending a chick or were sighted infrequently, indicating their colony attendance pattern was disrupted. Regular cycling patterns were obtained for 9 females, 22 males and 26 birds of unknown sex between July/September and 7 December (Table 5.5, Figure 5.7). Although these birds had been handled for either plumage dyeing, attachment of devices, injecting with tritium or stomach flushing, their cycling patterns were both regular and similar to each other; presumably the birds behaved normally on release. The females and males returned to the colony from foraging trips on 7.8 ± 0.4 and 7.4 ± 0.5 occasions, respectively (Table 5.5). As the field season ended about one week before the beginning of fledging (in mid-December), and the penguins' cycle time was <10 days at the time, the adults probably visited the colony at least once more after my departure. This additional visit would take the total number of foraging trips by females and males to about 9 and 8, respectively, during the five month period of chick development.

At Taylor Glacier, the remote attendance receiver never detected seven of the deployed transmitters and I suspect these units were poorly attached and lost at sea. A further 12 birds were detected infrequently due to either malfunctions with the equipment or disruption to the birds' normal chick rearing behaviour. Frequent and regular cycling patterns were recorded for three females and eight males (Table 5.5). Between mid-September and late November all but one penguin made four visits to the colony; the anomalous bird, a male, made seven visits. Over the same time period Auster penguins also averaged four visits to the colony. The similar frequency of foraging trips between birds from the two colonies suggests trip durations and attendance frequencies are not the reason for the disparity in size between the colonies, Taylor Glacier containing 70% fewer breeders than Auster.

Female emperors returning to Auster at hatching in July and August brooded their chicks for 18.8 ± 5.5 days, the reciprocal of which was the duration of the fast-breaking trip of the males (17.7 ± 3.8 days; Table 5.5, Figure 5.7).

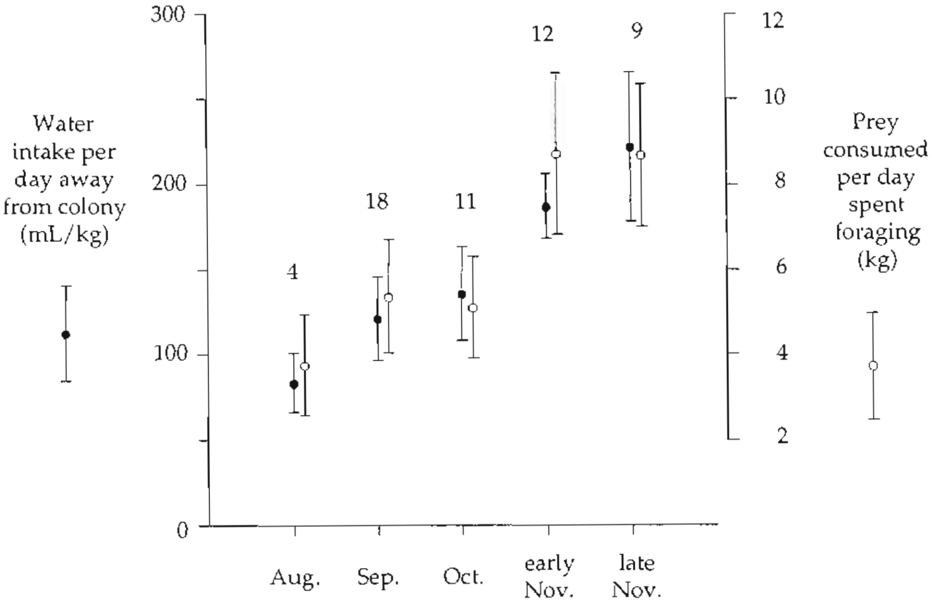


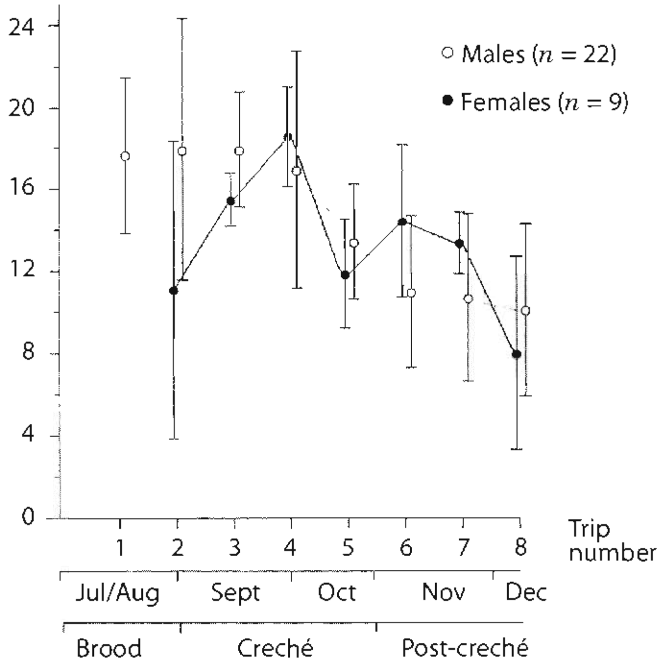
Figure 5.6 *Water intake per day away from the colony and prey consumption rates per foraging day of emperor penguins foraging during different months. Foraging days per trip were determined by TDRs during August, September and October, and estimated during November (see text). Data are means ± i SD and error bars are capped by the number of penguins sampled.*

The females then departed and foraged at sea for 8.7 ± 2.7 days which was similar to the period of chick brooding recorded for the males (11.4 ± 2.9 d). When relieved of the chick by the females for the second time, the males departed for 18.0 ± 6.4 d; however the females brooded the chicks for just 9.0 ± 2.6 days before leaving the chick unguarded at the colony. Therefore, parents brooded their chicks for about 40 days (38 ± 3 d, $n = 7$ penguins) in addition to the time the male brooded the newly-hatched chick while awaiting the arrival of the female from her long winter trip. During brooding the chicks received three food deliveries, two from the female and one from the male.

After leaving the chicks unguarded, foraging trip durations by the parents were similar between the sexes, and between parents at the two colonies (Table 5.5, Figure 5.7). The trip durations gradually decreased from 15–19 days in September to 11–15, 9–14, 8–13 and 4–10 days in October, early November, late November and early December, respectively. Periods of attendance at the colony also shortened from about 3 days in September to between 0.5 and 2 days in October, November and December.

Combining the data on foraging trip frequencies and durations with prey consumption rates provides an estimate of the amount of prey consumed by the parents during chick raising (Table 5.6). Between late July and early December, each pair that raised a chick to pre-fledging age consumed approximately 880 kg of prey, about 470 kg by the male and about 410 by the female.

(a) Foraging trip durations



(b) Colony attendance durations

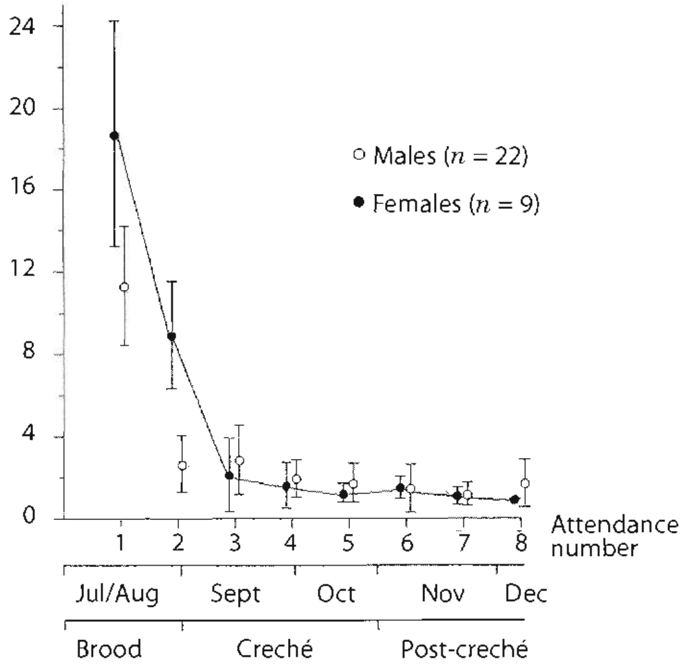


Figure 5.7 *Foraging trip (a) and colony attendance (b) durations of female and male emporer penguins that raised chicks at Auster Colony during 1993 (see Table 5.5).*

***Table 5.5** Cycle times of breeding emperor penguins from Auster and Taylor Glacier Colonies in 1993.*

Colony	Sex	Penguins		Development stage of chicks plus durations in days that parents spend in the colony (C), and on foraging trips (F)																		[b]Food
		penguins		Brood				Early-crèche			Late-crèche			Post-crèche to fledging								deliveries
		n		C	F	C		F	C	F	C	F	C	F	C	F	C	F	C	F	C	(*n*)
Auster	Female	9	[a]x̄	18.8	8.7	9.0		15.5	2.2	18.6	1.7	11.9	1.3	14.4	1.6	13.4	1.2	8.0	1.0			7.8
			±SD	5.5	2.7	2.6		1.3	1.8	2.4	1.1	2.7	0.5	3.7	0.5	1.5	0.4	4.7	<.1			0.4
				F	C	F	C															
	Male	22	x̄	17.7	11.4	18.0	2.7	18.0	2.9	17.0	2.0	13.5	1.8	11.1	1.5	10.8	1.3	10.2	1.7			7.4
			±SD	3.8	2.9	6.4	1.4	2.8	1.7	5.7	0.9	2.8	0.9	3.7	1.2	4.1	0.6	4.2	1.1			0.5
	Unknown	26	x̄					18.1	2.3	18.8	2.1	12.8	1.4	11.5	1.3	9.3	1.2	5.2	1.0	5.3	1.5	7.8
			±SD					3.8	1.3	7.4	1.4	3.0	0.8	3.0	0.8	2.9	0.5	3.6	<.1	2.8	1.0	0.7
Taylor Glacier																						
	Female	3	x̄						2.9	15.2	1.9	15.2	1.0	8.7	1.0							6.0
			±SD						0.2	4.9	1.3	5.6	0.8	6.6	0.6							<.0.1
	Male	8	x̄					16.5	2.6	16.8	1.7	12.4	1.9	9.0	0.7	7.8	0.5	8.5	0.8	2.4	0.8	6.4
			±SD						1.3	3.8	1.2	4.7	2.3	5.1	0.2	3.2	0.2					1.0
Feed no.																						
(F=Female, M=Male)				F1		F2			F3/		F4/		F5/		F6/		F7/		F8/		F9/	
					M1		M2		M3		M4		M5		M6		M7		M8		M9	

[a]Durations were not always recorded for all the penguins. On each occasion, means ±1 SD pertain to 60-100% of the penguins.

[b]Food loads delivered between hatching and 7 December at Auster, and between early-crèche and 26 November at Taylor Glacier.

5.4 Discussion

5.4.1 Foraging location

During late winter and spring in 1993, fast ice covered much of the continental shelf waters along the Mawson Coast. This ice forced the emperor penguins from Auster and Taylor Glacier to forage either in polynyas over the continental slope (the slope polynya), or in pack-ice regions further offshore. Auster penguins may also have foraged in shelf waters >80 km to the east of the colony. The slope polynya was assumed to be the birds' primary foraging area for a number of reasons. Firstly, the single tracked penguin foraged in the polynya during August. Secondly, antarctic krill and glacier squid dominated the penguins' diets and are at their greatest abundances in the vicinity of the slope (Miller and Hampton 1989, Lu and Williams 1994). Thirdly, the polynya was the closest open water to the colonies, and I suspect the breeding penguins would forage as close to their colony as possible to facilitate their regular return to feed chicks. Two satellite-tracked emperor penguins from Auster in the 1993 winter also foraged over the continental slope (Chapter 4). Slope regions are highly productive areas as a result of nutrient upwelling (Hempel 1985) and it is likely that emperor penguins should forage there during chick rearing.

In early summer 1993, the break-out of fast ice east of Auster exposed open water within 50 km of the colony. The ice break-out coincided with a change in the penguins' diet from primarily glacier squid to a range of outer shelf bentho-pelagic or under-ice fish (*Trematomus* species and *Pagothenia borchgrevinki*), and a four-day reduction of the Auster penguins' trip durations (from 8–13 to 4–10 d). Before and after the break-out, the penguins' direction on departing the colony did not change. The ice break-out provided the penguins with an opportunity to forage closer to the colony at a time when large, pre-fledging chicks were requiring more frequent food deliveries. It was suspected many penguins took this opportunity and foraged over the outer continental shelf during early summer.

5.4.2 Seasonal trends in diet

The diet of emperor penguins on the Mawson Coast in 1993 went through three distinct phases. First was a krill phase that lasted from late winter to mid-spring; the penguins also mainly ate krill in early and mid-winter 1993 (Chapter 4). Second was the squid phase in late spring when the main prey was a single cohort of immature and rapidly growing glacier squid. Third was a fish phase in early summer when Auster penguins ate mainly shelf-dwelling fish species after the sea ice break-out east of the colony in early summer, as mentioned above. Between the krill and squid phases, the diets changed gradually. Perhaps the immature glacier squid, which live at shallow depths (Piatkowski et al. 1990, Lu and Williams 1994), became more available, or they became more attractive prey items as their body sizes increased. Alternatively, krill may have become increasingly harder to catch, either forming looser schools or being progressively depleted within the penguins' foraging grounds. In contrast with the gradual change from krill to squid, the diet change from squid to shelf-dwelling fish in early summer was abrupt and probably caused by the sea ice break-out in late November.

Table 5.6 *Estimated average prey consumption by emperor penguin couples that successfully raised chicks. Consumption rates are per day away from the colony rather than per foraging day.*

Trip no.	Approx. period	Consumption per day away (kg)	Days per trip		Prey consumed per trip		
			male	female	male	female	total
1	Jul. - Aug.	2.6	18	[a]	47		47
2	Aug.	2.6	18	11	47	29	76
3	Sep.	3.4	18	16	61	54	115
4	Sep. - Oct.	3.4	17	19	58	65	123
5	Oct.	4.0	14	12	56	48	104
6	Oct. - Nov.	4.0	11	14	44	56	100
7	Nov.	5.7	11	13	63	74	137
8	Nov. - Dec.	6.8	10	8	68	54	122
9	Dec.	6.8	4	4	27	27	54
	Total				470	410	880

[a] The females' first foraging trip was during winter while males incubated the eggs.

In 1988 on the Mawson Coast, there was no obvious seasonal progression in the emperor penguins' diet between winter and early summer (Robertson et al. 1994a). Squid and shelf-dwelling fish species dominated the diets on all sampling occasions in 1988, with krill representing only a minor component of the diets (Robertson et al. 1994a). Comparing sea-ice images between years, in 1988 (Robertson 1994) the continental shelf was more ice-free than it was in 1993. The penguins probably ate shelf-dwelling fish in 1988 because they were available close to the colony, although a scarcity of krill in the slope region may also have induced the birds to forage over the shelf in that year. Krill can exhibit huge interannual fluctuations in abundance, affecting the foraging behaviours of many antarctic predators (Croxall et al. 1988b). The lack of a seasonal progression in diet during 1988 contrasts with the distinct seasonal trend in diet during 1993, but signals a substantial interannual variation in the diet of emperor penguins from the one location.

Few studies elsewhere have investigated the seasonality of emperor penguin diet. At Amanda Bay (69°17'S, 76°46'E) during chick raising in 1986, the penguins, diet was sampled three times between September and November and always comprised >80% antarctic silverfish, indicating there was little change in the diet during the study (Gales et al. 1990). At other locations, single season studies have discovered a variety of prey compositions. Off Adélie Land (66.5°S, 140°E) during spring, 95% of the penguins' diet was small nototheniids (possibly antarctic silverfish or *Trematomus* species; Offredo and Ridoux 1986).

At Dreschler Inlet in the Weddell Sea (72°52'S, 19°25'W) krill constituted 52% of the emperor penguins' diet in spring 1986 (Klages 1989) and 25% of the diets in late summer in both 1990 and 1991 (Pütz 1995). Fish species like antarctic silverfish and *P. borchgrevinki* comprised 75% of the diets at Dreschler Inlet in the 1990 and 1991 summers. The variability of diet between locations emphasises the diversity of the emperor penguins' foraging ability and also the complexity of their trophic relationships. Regular prey of the emperor penguins appear to be predominantly pelagic species which exhibit variable distributions, such as antarctic krill, antarctic silverfish and glacier squid (Everson 1983, Hubold 1984, Lu and Williams 1994). Irregular availabilities of these prey between seasons, years and locations is probably reflected in the penguins' fluctuating diet mix, and highlights the importance of prey switching by emperor penguins to satisfy their food and energy requirements.

5.4.3 Links between prey and diving behaviour

Krill were the main prey of the Auster emperor penguins between August and October (the first half of the chick raising period) and the birds dived most frequently to depths <100 m, suggesting the krill lived in abundance at these shallow depths. During August, in conjunction with foraging mainly at shallow depths, the penguins often dived to depths of greater than 100m. During September and October, as the proportion of squid in the diet increased, the penguins dived deep less frequently. A function of deep diving, which is more energetically demanding than shallow diving, may be to catch large bodied and potentially more nutritious prey that are not available near the surface (Costa 1991, Chapter 4). Perhaps, in September and October, the squid were sufficiently large and available in relatively shallow waters to supplement the krill, and obviate the penguins' need for deep diving.

Although larger bodied than the krill, squid taken by the penguins were still relatively small (25 g) compared with what the penguins are capable of catching (up to at least 500 g, Robertson et al. 1994a and this study). Much of the emperor penguins' prey were small bodied (i.e. <50 g), which conforms with the findings of several previous studies. For example, at Amanda Bay in 1986, Antarctic silverfish and glacier squid taken by emperor penguins averaged just 7 g and 3.8 g, respectively (Gales et al. 1990). The body sizes of different prey may influence the penguins' dive frequencies. In October in this study, to catch mainly krill weighing <1 g and squid weighing 25 g, the Auster penguins performed an average of 161.6 dives/d. In October 1988 when the diets comprised mostly fish and squid weighing 30–500 g, the penguins averaged 113.4 dives/d (Robertson 1994). Obviously, the penguins had to dive more frequently in 1993 than they did in 1988, to obtain their daily nutritional requirements.

5.4.4 Effect of day-length on foraging

As day length increased between August and October, the time taken by penguins to journey the same distance between the colony and the ice-edge reduced from approximately 8 to 2–3 d. The reduction was probably due to the penguins' travelling for more hours per day. Although nighttime travel by emperor penguins is possible (Ancel et al. 1992), the reduced light at night potentially slowed their rate of travel and often induced them to stop—indicated by a tendency for some birds to huddle at night during their outbound journey (see Chapter 6). The shorter travel times later in the year allowed the penguins to spend more days foraging which would reduce the time chicks had to wait between feeds.

While at sea the emperors exhibited a diurnal foraging pattern, resting on the sea ice at night and entering the water during the day. As day-length increased, their time spent foraging each day increased from approximately 8 hours in August to 13.0 hours in October. In winter, when periods of daylight are short, emperor penguins from Auster spent <5 hours in the water per day (Chapter 4) whereas in November, when periods of daylight were long, emperors in the Ross Sea foraged during all hours of the day (Kooyman and Kooyman 1995).

As day-length increases, emperor penguins dive more frequently, although dive frequency was also influenced by prey size and depth distribution as mentioned earlier. In early winter the penguins performed 62 dives/d (Chapter 4), in late winter and early spring the rates were 93–162 dives/d (this study) and in late spring a rate of 213 dives/d has been recorded (Kooyman and Kooyman 1995). The more dives performed per day enabled prey consumption rates and metabolic energy intakes to increase as the year progressed (see below).

Swimming time per day and dives per day, however, were not directly proportional to day-length because as day-length increased the penguins took more frequent and longer rest periods. Obviously, the penguins tire and/or reach satiation, such that rests are required to recuperate or to digest meals. The sea ice in antarctic waters provides a platform where the emperors can rest and be away from predators between diving bouts.

5.4.5 Seasonal changes in prey consumption rates

Male emperor penguins ate over twice as much prey per foraging day when providing for small chicks in August (4.0 kg) than did females foraging for self-maintenance in winter (1.8 kg/d, Chapter 4). While increasing day-length provides the opportunity for emperors to forage longer in spring and summer than in winter, increasing requirements of the birds probably provide an impetus for longer foraging. In August, the males had just broken a four month fast, had twice as many hours in which to feed as did the females foraging for self-maintenance during winter, and needed to return to the colony as soon as possible to brood and feed their chicks.

To provide for pre-fledging chicks in early summer, the adults apparently ate five times the winter, self-maintenance requirements of females. Although the demands on the adults peak at this time of year, and long periods of daylight provide ample time to forage, the consumption of 8.7 kg per day (30% of body mass) in early summer seems high. A potential source for error with the summer estimates was the prediction that the penguins took 1 day to cross the fast ice to the ice-edge. If it had taken the penguins half the predicted time (i.e. 0.5 d) to cross the fast ice the estimated prey consumption rates per foraging day would be about 7.6 kg. Without additional information on the trip durations, however, there was no reason to modify the calculated consumption rates simply because they seem high. Further study on the feeding rates of emperor penguins in summer is necessary to verify the findings presented here.

Each penguin pair at Auster that successfully raised a chick consumed approximately 880 kg of prey during chick raising. During winter while males were incubating eggs, females consumed about 100 kg of prey (Chapter 4); therefore between May and early December in 1993, each breeding pair that raised a chick ate about 980 kg of prey. This estimate is extremely close to the 965 kg required to raise a chick predicted by Robertson and Newgrain (1996), and suggests that about 1000 kg of food is required each breeding season to maintain two adults and raise one chick.

Apportioning prey types to the penguins' consumption rates during chick rearing in 1993, it was estimated that each pair of Auster penguins that raised a chick ate about 430 kg of antarctic krill, 210 kg of glacier squid, 100 kg of *Trematomus* species, 100 kg of antarctic silverfish, 40 kg of *Alluroteuthis antarcticus* and 100 kg of other prey (mainly fish). With about 11 200 chicks raised to fledging age in 1993 (Chapter 2), the successful parents consumed about 11 000 metric tons of food, a considerable biomass to be taken from the waters adjacent to the colony.

5.4.6 Food delivery to the chicks

The field work at Auster colony ended on 7 December, by which time most females that cycled regularly had returned to feed their chicks eight times and males had returned either seven or eight times. The chicks were expected to commence fledging approximately 1 week later (see Robertson 1992). As the adults' trip durations were 4–10 days in length in early December, both parents potentially delivered at least one more meal to their chicks prior to their fledging. Therefore, between hatching and fledging, the chicks probably received about 18–20 food deliveries. The chick attendance times and food delivery frequencies recorded at both Auster and Taylor Glacier colonies were similar to those recorded at the Pointe Géologie colony (66.5°S, 140°E) in the 1950s (Prévost 1961), and may be similar for all emperor penguin colonies.

There is a discrepancy between the food masses delivered by parents and the requirements of the chicks; emperor chicks require about 84 kg of prey to achieve fledging condition (Robertson 1994). With 18–20 food deliveries, the parents needed to average about 4 kg of food per delivery, but from stomach-flushed adults, mean wet masses of just 1.3 ± 0.6 kg were obtained. Mass gains by parents on foraging trips during the 4–5 months of chick raising invariably averaged 4 kg and during chick rearing the parents gained only a few kg in body mass, supporting the impression that approximately 4 kg of prey was delivered to the chicks on each visit. Perhaps stomach flushing was incomplete. Alternatively, much of the stomach contents could have been smaller than the diameter of the sieve. The volumes of food obtained in the present study were similar to those recovered in other studies of emperor penguin diet that employed 0.5 mm or 1.0 mm sieves (Klages 1989, Gales et al. 1990, Robertson et al. 1994a), but distinctly less than that recovered by Offredo and Ridoux (1986, 2.4 to 3.6 kg) who adopted a 0.25 mm sieve. Perhaps much of the stomach contents is in an almost liquid form which passed through the sieve. Future studies could solve this potential problem by employing smaller mesh sieves and accurately measuring the volumes of water administered and retrieved during flushing. Another potential explanation for the discrepancy is that chicks may have been fed by adults other than their parents, as described by Jouventin et al. (1995). Although observations of feeding by non-parents was rare (Jouventin et al. 1995), its potential role in chick survival and growth warrants further investigation.

In summary, the trophic interrelationships between emperor penguins raising chicks and their prey change seasonally in response to fluctuating sea ice conditions, differences in the prey availabilities, changes in day-length toward summer, and increasing demands of the growing chicks. A prey type targeted by the penguins at any given time could either be preferred over another prey type, or be the only prey available. Managers of fisheries in antarctic waters need to realise that the degree of direct competition between penguins and a fishery that removes the penguins' prey, will vary temporally and spatially. Also, the impacts on penguins of a fishery will vary, depending on whether or not there are alternative prey available to the birds.

6. THE OCCURRENCE AND PURPOSE OF HUDDLING BY EMPEROR PENGUINS DURING FORAGING TRIPS

6.1 Introduction

Despite large fluctuations in their environmental temperatures, birds and mammals maintain body temperatures within a narrow thermoneutral zone, which is the temperature range of least energy expenditure (Calder and King 1974; Kendeigh et al. 1977). Thermoregulation is controlled primarily by body insulation. Below a lower critical temperature, however, insulation alone is insufficient to maintain thermoneutrality and energy must be expended to produce heat (Le Maho et al. 1976; Kendeigh et al. 1977). To minimise the need for this energy expenditure, most birds and mammals adopt certain thermoregulatory behaviours. These behaviours may be individual, such as hibernation, or social and perhaps the most extreme example of social thermoregulation in a cold climate is the sharing of body warmth by huddling emperor penguins *Aptenodytes forsteri* during the antarctic winter (Prévost 1961).

Emperor penguins breed in winter on the Antarctic fast ice where air temperatures reach -40°C and wind speeds can exceed 200 km/h (Groscolas 1990). To conserve energy and minimise mass loss when fasting at the colony, emperor penguins form dense huddles of up to 10 birds/m^2 (Prévost 1961). This huddling behaviour is particularly important for male emperors which, during courtship and incubation (autumn to winter), fast for up to four months, living off fat reserves accumulated in the previous summer (Le Maho et al. 1977 Groscolas 1986). When huddling, emperor penguins lower their metabolic rates (Ancel et al. 1997) which reduces their rate of mass loss to about half that of non-huddling birds (Prévost 1961). Huddling is crucial to the survival of emperor penguins in Antarctica.

To date, huddling by emperor penguins has been observed only at their colonies (see Robertson 1990). Here, I provide evidence for huddling by emperors while on foraging trips away from their colonies. I also describe the frequency of these events and discuss the possible significance of away-from-colony huddling: could it serve a social or an energy conservation function?

6.2 Methods

This study was conducted in 1993 at the Auster (67°23'S, 64°04'E) and Taylor Glacier (67°28'S, 60°54'E) colonies, which lie 55 km east and 95 km west, respectively, of Mawson Station, Antarctica. Time-depth-recorders (TDRs, Mk 5, Wildlife Computers, USA) were secured to the lower backs of 56 emperor penguins departing these colonies to forage at sea, and recorded the penguins' diving behaviour (see Chapters 4 and 5). In addition, temperature and light sensors were positioned on the outside of the TDRs, away from the penguin's back, and recorded ambient conditions at 15 min intervals. The range of the temperature sensors was -2.3°C to 23°C, while light levels were recorded on an arbitrary scale which enabled differentiation between night and day.

TDRs were secured on 18 females after egg laying in May, 14 males breaking their winter fast in August, and 14 and 10 birds of unknown sex in September and October, respectively. All birds were weighed using spring scales to ± 0.1 kg. Foraging trips of the females in winter lasted about 70 days whereas the trips of the other instrumented penguins were of 2–3 weeks duration. To obtain records over the entire foraging trips of the females in winter, different TDRs were programmed to sample in the early, middle and late stages of the birds' foraging trips. This delay protocol was adopted again during August and September deployments, but proved to be unnecessary, so in October, all TDRs commenced recording immediately on deployment.

Penguins were relieved of the TDRs when they returned to their colony to attend their chicks. Some penguins passed us unnoticed and entered the colony with their TDRs, enabling us to record huddling events within the colony. Temperature and light readings obtained from these colony-based huddles could be compared with presumed huddling events away from the colony, to attest to the latter's authenticity.

Huddling events were defined as times when light levels recorded by the TDRs were at night-time levels, indicating either night-time or substantial shielding from the sun during day time, and the temperature rose above 0°C for at least 1 hour. High temperature events that were <1 hour in duration were ignored because these would have been under-sampled by the 15 min sampling interval, although in doing this I may have underestimated the frequency of huddles. The positive temperatures were anomalies in the antarctic environment in winter and spring, when ambient temperatures do not approach 0°C (rarely exceeding –15°C), and as they occurred in conjunction with low light levels, they could not have resulted from incident solar energy. In spring, despite negative air temperatures, incident solar energy on the TDRs occasionally did raise a sensor's temperature to >0°C, however these events were associated with high light levels. I presumed the low light/ high temperature occurrences registered that another bird was shielding and warming the back of the TDR-bearing penguin, which occurs when the birds huddle together. The huddling events were categorised by their month of occurrence (May to July, August, September, or October) and the penguins' location; outbound from the colony to the ice-edge (about 80 km away and requiring up to 9 days to reach), at sea resting on sea ice between foraging periods, or inbound from the ice-edge to the colony. As the TDRs also recorded instances when penguins dived, it was possible to distinguish temperature and light data recorded underwater from that recorded by birds standing on the sea-ice.

The accuracies of the TDRs' temperature and light sensors and internal clocks were tested before deployment and after retrieval by running the units for several days in a field hut. During these tests, I compared the sensors' readings with the times of sunrise and sunset, and ambient temperatures in the hut, measured with a mercury thermometer. The tests confirmed the accuracy of the sensors and internal clocks.

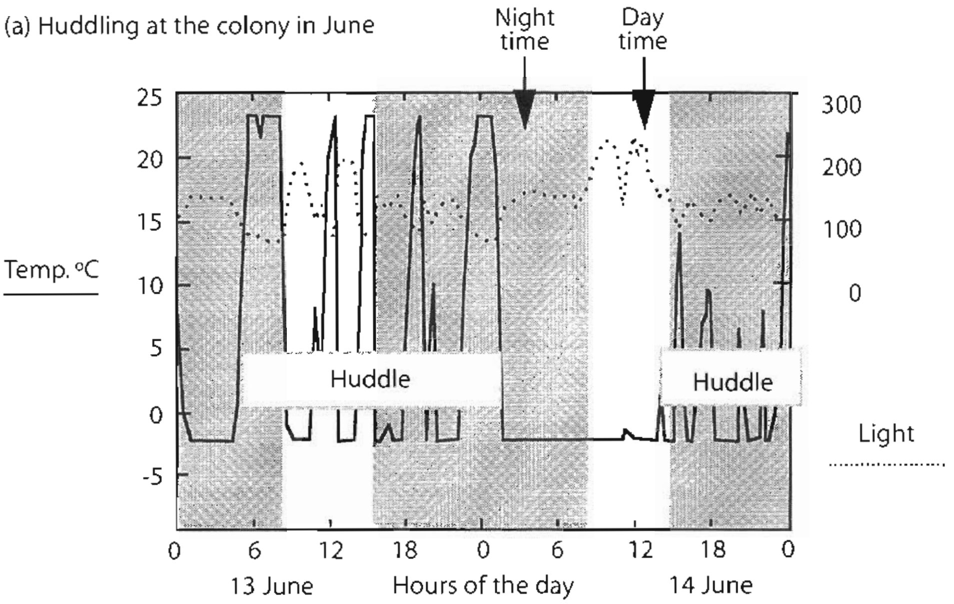
6.3 Results

During the study, sea-water temperatures measured by the TDRs ranged between -1.8 and 0.8°C and ambient air temperatures at Mawson Station ranged between -35°C and -15°C (Dept. of Meteorology, Hobart). Depending on a penguin's distance from the coast (0–100 km, see Chapters 4 and 5), it could have experienced air temperatures up to 5°C warmer than the temperatures recorded at Mawson.

TDRs were recovered from 50 penguins—four from Taylor Glacier females that foraged between May and July and the remainder from Auster penguins. The data from the two colonies were combined and treated as a time series, which included 14 females that foraged during May to July, 13 males on foraging trips in August, 13 penguins from September and 10 from October. In total, the TDRs sampled during 907 days, comprising 599 days in the period from May to July, 117 days in August, 105 days in September and 86 days in October.

The temperature and light recordings during the presumed away-from-colony huddling events were comparable with the sequences from known colony-based huddles. From the 907 days recorded, I identified 65 incidences of away-from-colony huddling; 41 by penguins outbound to the ice-edge, 19 by penguins at sea, and 5 by penguins inbound to their colony (representing 41%, 2.5% and 19% of days recorded for each location, respectively; Figure 6.1a-d, Table 6.1). The huddles usually occurred at night, although between May and August some huddles formed during the day. Occasionally, a penguin appeared to huddle several times in a single night, each event being separated by several hours of below zero temperatures (see Figure 6.1a); a series of huddling incidences within one night was assumed to be a single huddling event with the cold periods indicating times when the penguin left the huddle briefly, or when its back was exposed at the outer edge of the huddle. The maximum number of huddling incidences recorded for a single penguin was nine, and 21 (40%) penguins showed no evidence of huddling while their TDRs were sampling.

(a) Huddling at the colony in June



(b) Huddling on the out bound journey

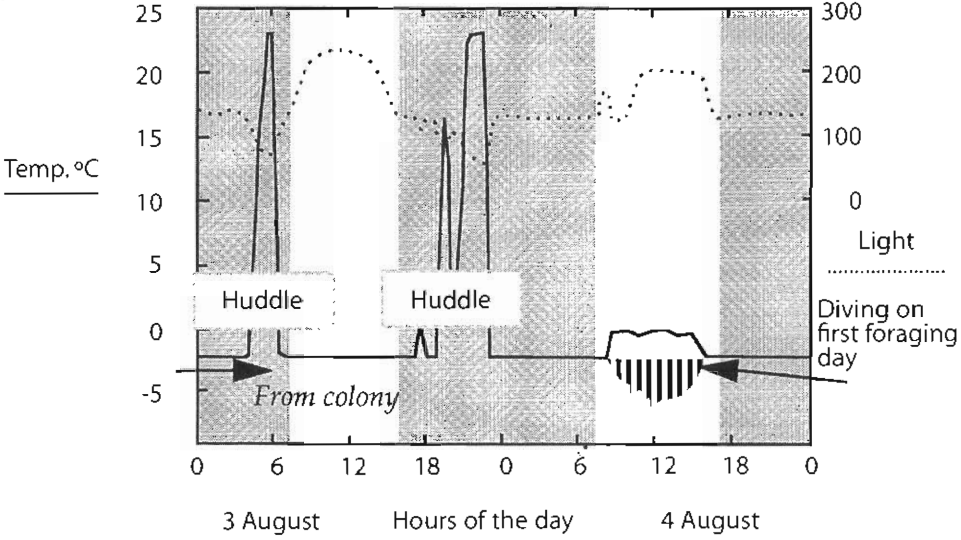
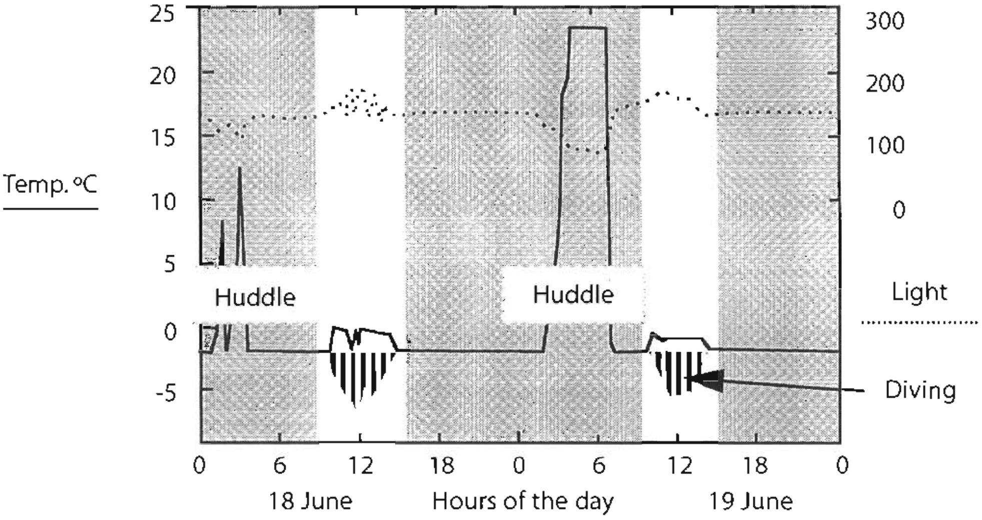


Figure 6.1 *Trends in temperature (°C) and light records from sensors on the backs of emperor penguins showing representative incidences of huddling; (a) at the breeding colony, (b) when journeying over fast-ice from the colony to the ice-edge, (c) while resting on sea-ice between foraging days, and (d) when inbound over the fast-ice from the ice-edge to the colony. Light levels were recorded on an arbitrary scale of 0 (no light) to 250 (strong sunlight).*

(c) Huddling at sea



(d) Huddling on the inbound journey

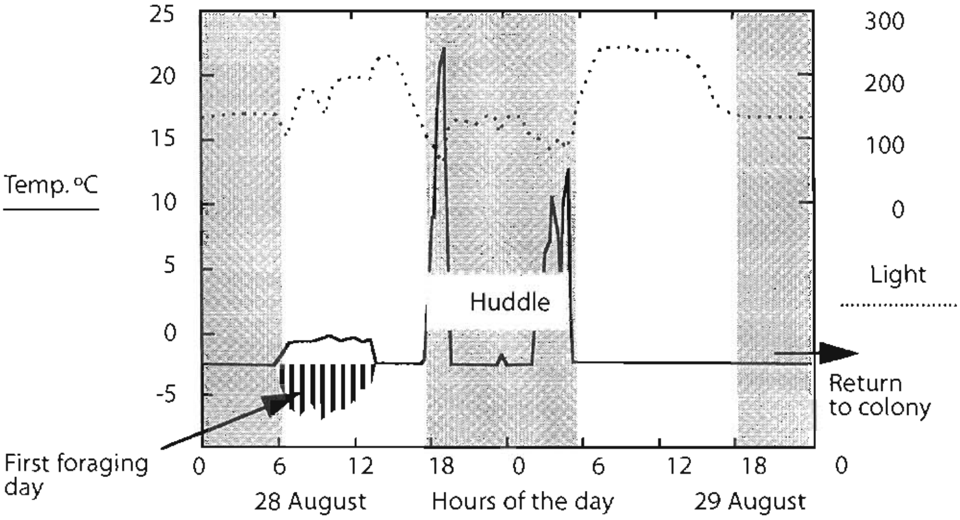


Figure 6.1 (continued)

Five of the TDRs deployed on females in May sampled during the penguins' outbound journeys. All five of the penguins that carried these TDRs huddled on at least half of the nights of their outbound journey (Table 6.1), including on the night before they entered the sea. One bird huddled on seven of the eight nights of its journey to the ice-edge. Of the 14 females that carried TDRs during June and July, four huddled (2, 2, 4, and 9 times), with no incidences of huddling recorded for the remaining 10 penguins. During return journeys to the colony in late July/early August, only five TDRs were recording, and two of the five females that carried these TDRs huddled on the night after their exit from the water. The other three penguins did not huddle during their inbound journeys.

In August, outbound journeys for six males were sampled, with three of these birds huddling on the night before they entered the water (one of the three birds also huddled one night when it was mid-journey; Table 6.1). The other three males did not huddle during their outbound journeys. Of the 13 males for which at-sea records were obtained in August, only one huddled and did so on only one occasion. Two of three males for which inbound records were obtained huddled, both doing so on the night after they left the water; one of the two also huddled on the night before it arrived at the colony. In September, nine of the 13 penguins that carried TDRs were monitored during their outbound journey, and seven of the nine huddled, primarily on the night before entering the water. One of the 13 September penguins huddled at sea (once) and no records were obtained for return journeys in this month. In October, two of the 10 penguins huddled during their outward journey, both doing so on the night prior to entering the water; no penguins showed evidence of huddling at sea, and no data were obtained for return journeys. In summary, incidences of huddling away from the colony were rare, although females when outbound in May and June commonly participated in huddles, as did many birds on their arrival at the ice-edge,.

During their outbound journeys in winter, lighter birds tended to huddle more frequently than did heavier birds, but still had similar or even shorter trip durations. For example, the lightest female departing Auster in May (23.8 kg) huddled on seven of eight nights (88%) before entering the water, whereas the heaviest female (29.2 kg) huddled on five of nine nights (56%). Likewise, the lightest male departing Auster in August (22.0 kg) huddled on one of two nights, whereas the heaviest males (both 24.5 kg) did not huddle during their journeys (two and five nights).

Penguins on foraging trips huddled for shorter periods as the months progressed; 6.3 ± 4.4 h per huddle in May/July, then 2.5 ± 1.0 h, 2.2 ± 1.7 h, and 1.4 ± 0.2 h per huddle in August, September, and October, respectively. The longest huddling event was 15.5 hours by a female the night before she entered the water in early June.

In addition to huddling events away from the colony, 27 incidences of huddling at the colony were identified: six in May by a female that spent 9 days at the colony after TDR attachment, and in August, six, seven and eight incidences by males for which 6, 11 and 9 days, respectively, were sampled at the colony by the TDRs. In both May and August, the durations of huddles at the colony (12.2

Table 6.1 *Days sampled and huddling events recorded by temperature/light sensors that were attached to the backs of Emperor Penguins when they departed Auster or Taylor Glacier Colony. The huddling events performed by each penguin are summaries according to the month and location of their occurrence. The penguins' locations were; outbound between the colony and the ice-edge, at sea, and inbound between the ice-edge and the colony. '-' indicates no days sampled.*

Month & location	days sampled and huddles recorded for individual penguins															Totals
May-July	Penguin	1	2	3	4	5	6	7	8	9	10	11	12	13	14	14
Outbound	days	8	8	8	9	-	-	-	-	-	-	6	-	-	-	39
	Huddles	6	5	7	5	-	-	-	-	-	-	3	-	-	-	26
At sea	days	56	71	24	23	40	40	31	28	35	30	54	43	37	30	542
	Huddles	2	0	0	0	2	0	0	9	0	0	4	0	0	0	17
Inbound	days	-	6	-	-	-	-	2	-	5	-	-	-	3	2	18
	Huddles	-	1	-	-	-	-	0	-	0	-	-	-	0	0	1
August	Penguin	1	2	3	4	5	6	7	8	9	10	11	12	13		13
Outbound	days	-	-	5	4	4	2	-	2	2	-	-	-	-		19
	Huddles	-	-	0	2	1	0	-	0	1	-	-	-	-		4
At sea	days	4	9	8	4	9	8	10	10	5	5	8	2	8		90
	huddles	0	0	0	0	0	1	0	0	0	0	0	0	0		1
Inbound	days	-	-	-	-	-	5	-	-	-	-	-	2	1		8
	Huddles	-	-	-	-	-	1	-	-	-	-	-	2	0	3	
September	Penguin	1	2	3	4	5	6	7	8	9	10	11	12	13		13
Outbound	days	2	2	2	2	3	4	2	3	2	-	-	-	-		22
	Huddles	1	0	1	3	1	1	0	1	1	-	-	-	-		1
No inbound days sampled																
October	Penguin	1	2	3	4	5	6	7	8	9	10					10
Outbound	days	2	2	2	2	2	2	2	2	2	2					55
	Huddles	1	0	1	0	0	0	0	0	0	0					2
At sea	days	6	7	9	8	7	7	6	5	6	5					66
		No huddles at sea recorded														
		No inbound days sampled														

± 7.4 hours in May and 8.8 ± 8.8 hours in August) were significantly longer than the durations of huddles away from the colony (Unpaired *t*-tests; $t = 2.85$, df = 49, $P = 0.006$, in June/July; $t = 2.23$, df = 28, $P = 0.034$, in August). The longest recorded huddling incidence at the colony, 30 hours, was performed by a penguin in August.

6.4 Discussion

Huddling by emperor penguins was seen by observers only at the colonies and the interpretation of huddling events away from colonies was based on the data obtained from TDRs. However, huddling with other penguins is the only plausible explanation for the recorded low light levels and positive temperatures when ambient temperatures were -15°C to -35°C. While the number of penguins forming huddles is unknown, judging by the TDR temperature changes and the gregarious nature of emperor penguins, between several and hundreds of penguins may have been involved; at sea this could signal a major concentration of birds.

Huddling away from the colony probably serves to conserve energy, when the alternative for penguins gathered together is to stand in isolation. To assess the energy conservation value of huddling, I examined the energy saving through huddling by females leaving the Auster colony in May, when most away-from-colony huddles occurred. These females averaged 25.4 ± 1.8 kg in body mass ($n = 25$, Chapter 4), 2.4 kg more than the critical body mass (23 kg) below which protein catabolism commences in fasting emperor penguins, and 7 kg more than the lethal body mass (18 kg; Groscolas 1990). Hence most females left the colony with considerable energy reserves. By stopping, as indicated by the huddles, the females extended the duration of their fast by approximately 1.3 days (five huddles x 6.3 h/huddle, the mean frequency and duration recorded). Presumably the stops were necessary and possible reasons for them are discussed below. The delay to the birds' arrival at the ice-edge, however, could have cost them approximately 5,135 kJ of energy (self maintenance metabolism, 155.5 kJ/kg/d, Ancel et al. 1997, for a 25.4 kg bird over 1.3 d), equivalent to the metabolism of approximately 130 g of fat (assuming fat was the only metabolite and fat yields 39.4 J/g, Groscolas et al. 1991). Since birds in huddles lose mass at half the rate of isolated birds (Prévost 1961), by huddling during the stops, the birds reduced the energetic costs of their breaks in travel by approximately 50%.

The conservation of 65 g of fat, while representing a desirable saving to birds in healthy condition, may be critical to the survival of birds in poor condition. When outbound from their colony in winter, birds with body masses near to or below the lower critical mass of 23 kg tended to huddle more frequently than did heavier birds. Perhaps this was a consequence of the lighter birds' need to conserve energy, i.e. lighter birds sought out huddles more than heavier birds. Interestingly, lighter birds had similar or shorter trip durations than did heavier birds, suggesting lighter birds either rested for shorter durations or, when moving, travelled at faster speeds.

In addition to their energy conservation value, away-from-colony huddles may serve a social purpose; they may reaffirm a behaviour that is required for survival at the colony. An instinct of emperor penguins standing in a group during cold periods may be to form a huddle, regardless of the birds' requirements for energy conservation at the time.

The frequency and location of away-from-colony huddles provides an indication of when and where groups of penguins stopped and rested. Overall, the penguins rarely huddled away from their colony suggesting they rarely stopped and rested in large groups during foraging trips. Exceptions were the regular huddles of females journeying to the ice-edge after completing their two-month courtship and egg production period, and huddles by penguins of either sex on their arrival at the ice-edge. In May, females departed their colony in groups. Travelling in groups may have enabled the birds to share the burden of trail-making and ensured sufficient females were present to form a huddle when conditions made this desirable. During the journey, the females probably had reasons to stop which were precursors to their forming huddles. Perhaps they stopped because of navigation difficulties during the long winter nights or during adverse weather conditions, such as blizzards and extreme cold. Alternatively, the females could have tired quickly while crossing the newly formed fast-ice and needed breaks to recuperate energy. Just after formation, fast-ice is slippery and rafted and could be arduous for penguins to traverse compared with later in the year when hardened snow adds grip and evens out much of the rafting. Also, these females had just laid their eggs and could have had difficulties walking for long periods. A further consideration is that the females were departing for two months and did not need to return to the colony quickly to provision their chicks. Later in the year, the requirement to feed chicks perhaps stimulated parents to travel during severe weather conditions, rather than rest and await an improvement.

The frequent huddling at the ice-edge suggested that penguins tended to gather at this location. Benefits of gathering at the ice-edge before returning to the colony would be comparable to those for out-bound birds, i.e. sharing the burden of trail-making and facilitating huddles during their journey. A benefit of gathering before entering the sea is that the penguins then could enter in large numbers, minimising each individual's chance of being ambushed by a predator, such as a leopard seal *Hydrurga leptonyx* or a killer whale *Orcinus orca*.

Future deployments of back-mounted temperature and light sensors on emperor penguins will provide a better understanding of the frequency and energy conservation value of huddles, and will increase our knowledge of the thermoregulatory behaviour of this unusual bird. Such studies would benefit from the use of more frequent sampling rates than our 15 min intervals and from temperature sensors with broader ranges than -2.3°C to 23°C.

Appendix 6. An approximation of the energy saved by huddling at nights during travel to the ice-edge, by female emperor penguins departing Auster colony in May.

The energy cost of travelling to the ice-edge equals the energy cost of walking to the ice-edge plus the energy cost of self maintenance. The energy saved by huddling during the journey equals the energetic cost of remaining in isolation minus the sum of the energy cost of huddling for a total of 1.3 days (i.e. 5 huddles each 6.3 hours in duration, see text) and the energy cost of remaining in isolation for the rest of the journey,

i.e.

$$E_{saved} = [E_w + E_{m}t] - [E_w + E_{h}d + E_{m}(t\text{-}d)] \qquad \text{(equation 6.1)}$$

where;

E_{saved} = energy saved by huddling during the outbound journey.

E_w = energy cost of walking to the ice-edge, which is the mass-specific cost of walking times the distance travelled. Thus a 25.4-kg (see text) bird expending 17.5 $J/kg{\cdot}m^{-1}$ (Dewasmes et al. 1980) walking the 80 km to the ice-edge would expend 35,560 kJ.

$E_{m}t$ = energy cost of self maintenance in isolation for the journeys' duration (time t), which is the product of resting metabolic rate and the duration of the journey. Thus: 25.4 kg x 155.5 $kJ/kg{\cdot}d^{-1}$ (Ancel et al. 1997) x 8 days (Chapter 4), or 31,598 kJ.

$E_{h}d$ = energy cost of self maintenance when in huddles (time d, i.e. 1.3 d). Huddling metabolism (i.e. 77.8 $kJ/kg{\cdot}d^{-1}$) is approximately half that of non-huddling metabolism (see above), assuming huddling birds lose mass at half the rate of isolated birds (Prévost 1961). Hence, huddling metabolism = 25.4 x 77.8 x 1.3, or 2569 kJ.

$E_{m}(t\text{-}d)$ = energy cost of self maintenance when not in huddles (time t-d, i.e. 8-1.3 = 6.7 d), which equals 25.4 x 155.5 x 6.7, or 26,463 kJ.

Based on equation 1, the energy saved by huddling was 2556 kJ. Assuming fat yields 39.4 J/g (Groscolas et al. 1991) and that fat was the only metabolite, the energy saving would be equivalent to about 65 g of fat.

7. General discussion

This study was driven by the need to increase our understanding of trophic relationships in antarctic waters. Human exploitations in antarctic waters, and other marine environments, have regularly led to over-exploitations and detrimental impacts on ecosystems, with many of the impacts being difficult to interpret due to a poor prior knowledge of trophodynamics within the ecosystem (Agnew and Nicol 1996, Walters and Maguire 1996). Food webs and community dynamics are more complex than is suggested by single linear chains, on which much of the theory of trophodynamics is based (Polis and Strong 1996), and current thinking proposes that an ecosystem management approach will improve our ability to conserve environments where we exploit resources (e.g. Knecht and Cicin-Sain 1993, Larkin 1996). With this in mind, the central aims of the present study were to assess the foraging ecology of adult emperor penguins, to predict resource requirements of these seabirds and in doing so, to improve our understanding of trophic relationships involving emperor penguins in antarctic waters.

Detailed discussions of the results and avenues for future research have been presented in the previous chapters. In this general discussion, I briefly highlight the main findings of the study which are presented in Chapters 2, 4 and 5, and discuss the role of emperor penguins in antarctic marine ecosystems.

The 1993 breeding period was a relatively profitable one for emperor penguins at the Auster and Taylor Glacier colonies on the Mawson Coast. Although there have been few quantitative assessments of population size and breeding success at these colonies, in 1993 there were more breeding pairs and more chicks fledged than have previously been recorded there, and the breeding success of 84% was amongst the highest reported for an emperor penguin colony (Budd 1962, Jouventin and Weimerskirch 1991, Robertson 1994). The high number of breeding pairs and breeding success suggest that on the Mawson Coast in 1993, food availability was high both before and during chick rearing.

During winter and spring, it was presumed that many emperor penguins from the Auster colony foraged less than 150 km from the colony (Chapters 4 and 5), despite their capacity to travel considerably greater distances (Ancel et al. 1990). This presumption was supported by a study of 21 emperor penguin foraging tracks in 1994 (Wienecke and Robertson 1997) which found that most penguins from Auster colony foraged in the same vicinity as did the three penguins that were tracked in the present study. Sufficient resources apparently were available to the penguins this close to the colony to negate the need to travel greater distances. During winter foraging, the females consumed approximately 1.8 kg of prey per day with their diet comprising mainly antarctic krill (*Euphausia superba*), approximately 70% of the diet. Males foraging in late winter, after their long incubation fasts, consumed approximately 4.0 kg of prey per day and again were eating mainly krill (68% of their diet). As day-length increased toward summer the parents, who apparently feed only during daylight hours, foraged during more hours of the day. The increased demands of their growing chicks probably stimulated them to forage more. The penguins' consumption rates increased from 5.4 kg per day in September to 8.7 kg per day in November. Through this time their diets changed, with the proportion of krill in the diets decreasing and the proportion of squid—both glacier squid (*Psychroteuthis glacialis*) and *Alluroteuthis antarcticus*—increasing. In November, the birds were consuming mainly glacier squid (approximately 60% of their diet). Either krill became less available over time, or squid became more available, and the penguins adapted their foraging strategies accordingly.

In late November, a large section of fast ice, that had covered the outer continental shelf east of Auster, broke away, allowing penguins access to prey resources closer to the Auster colony. A change in the penguins' diet to a suite of principally shelf-dwelling fish species (including *Trematomus* spp and *Pagothenia borchgrevinki*) demonstrated that the birds had taken the opportunity to forage closer, thereby reducing the travel component of their foraging trips.

The dietary progression described above highlighted two things. Firstly, it emphasised the variability of the emperor penguins' foraging repertoire. This was also demonstrated by the vast degree of individual variability in diving behaviour and diet of penguins foraging concurrently at certain stages during the breeding period (see Chapters 4 and 5). Secondly, the progressive change in diet highlighted the limitations of dietary studies during single seasons. These 'snap-shots' of diet give unrealistic, and perhaps overly simplified pictures of the emperor penguins' trophic relationships.

Combining data from females during incubation and both sexes during chick rearing, in 1993, each breeding pair that raised a chick to fledging age consumed 980 kg of prey. As 1993 apparently was a good year for the emperor penguins on the Mawson Coast, the high chick survival was probably influenced by a better-than-average abundance and/or availability of prey, particularly krill. This availability contrasts with other evidence that suggests krill were scarce in 1993. Zooplankton surveys in the vicinity of the Mawson Coast in early 1993 found that the distribution of krill was restricted compared with previous years (Hosie 1994, Hosie and Cochran 1994, Hosie et al. 1997). Hosie et al. (1997) suggested that krill had either declined in the area or altered their distribution patterns, perhaps in response to persistent southward air-flows, which are thought to influence krill distribution in the Atlantic sector of the Southern Ocean (Priddle et al. 1988). In addition, exceptionally high mortalities of Adélie penguin (*Pygoscelis adeliae*) chicks at colonies near Mawson Station during the 1993/94 austral summer may have been caused by a paucity of krill in the area (Kerry et al. 1995b). In the winter of 1993, between the two summers of apparent low krill abundance, the bounty of krill in the diets of emperor penguins, and the penguins' propensity to forage at depths <100 m, suggests krill were present and should have been available to both the zooplankton survey nets, that sifted water between 0–200 m deep, and Adélie penguins, which can dive to 200 m deep. Perhaps, in 1993, the krill moved into deeper water during summer months, despite usual prevalence at depths <100 m at this time of year (Siegel 1985, Higginbottom and Hosie 1989, Godlewska 1993). At times, however, krill can be abundant at depths >200 m (Duhamel and Williams 1990), and a shift from a shallow winter distribution to a deep summer distribution during 1993 could explain not only the diminishing abundance of krill in the emperor penguins' diet as summer approached, but also the reduced availability of krill to the summer net surveys and breeding Adélie penguins. Obviously, interseasonal and interannual variability in prey abundance and distribution will influence the breeding success of higher predators in the antarctic marine environment, and such trophic interactions require further study.

A review of the research on the diets of emperor penguins, the facet of emperor penguin foraging ecology that has been most studied, emphasises the diversity of the penguins' foraging ability (Table 7.1). Several studies highlight the importance of krill to emperor penguins (Klages 1989, this study), which is not surprising considering the enormous abundance of krill in antarctic oceans (Everson 1982). Krill are an important prey of many antarctic higher predators, including other penguin species (Croxall and Furse 1980, Croxall and Prince 1984, Ridoux and Offredo 1989), many fish species (Williams 1985), petrel species (Reid et al. 1997), antarctic fur seals (*Arctocephalus gazella*, Reid and Arnould 1996), crabeater seals (*Lobodon carcinophagus*, Øritsland 1977) and baleen whales (Ichii 1990, Klinowska 1991). In addition to krill, the Antarctic silverfish (*Pleuragramma antarcticum*) constitutes varying proportions of the emperor penguins' diets; averaging 7% per month (but up to 15%, in the present study and 8% on the Mawson Coast in 1988 (Robertson et al. 1994a)), to approximately 78% at Amanda Bay 1986 (Gales et al. 1990). Antarctic silverfish are also a major prey of Weddell seals (*Leptonychotes weddelii*, Plötz 1986, Green and Burton 1987). The squid *P. glacialis* is a common component of the emperor penguins' diet and is consumed by other antarctic predators such as Adélie penguins (Offredo et al. 1985) and elephant seals (*Mirounga leonina*, Rodhouse et al. 1992, Slip 1995). Given the potential of competition for prey with other predators and the patchy and apparently seasonal distribution of their pelagic prey, it is advantageous for the emperors to have flexible foraging strategies.

Emperor penguins are, therefore, well adapted to their antarctic environment, with both their winter breeding capacity and their adaptable foraging ability. Amongst birds, unusual life-history strategies appear to be promoted by extreme conditions. The adaptability of their life-history strategies has enabled birds to inhabit a broad range of environments, and the emperor penguin represents an exceptional example of this adaptive radiation.

As a final comment, I wish to emphasise the value of multidisciplinary and multispecies approaches to the assessment of trophodynamics within ecosystems. Researchers often advocate the utility of particular species with which to monitor ecosystems, but this approach has disadvantages. Ecosystems are more complex than will be revealed by one avenue of research. For example, in Antarctica, a study of Adélie penguin foraging ecology will provide an indication of what is available to Adélie penguins, and not necessarily what is available to other species or abundant within the ecosystem. Such studies need to be linked with numerous pertinent factors, including local distribution and abundance of prey, the physiological capacity of the bird, past and present competition, breeding strategies and timetables and so on.

In an ecosystem management approach to marine conservation, numerically dominant or vulnerable species should not be studied exclusively, but rather, the roles of all species within an ecosystem should be considered. Having said this, to promote public awareness of an issue, key species are often needed to emphasise and model ecosystem changes. As the most cold-adapted bird and with a life-history strategy that will always instil wonder and intrigue, the emperor penguin could represent a flagship species for antarctic ecosystems research.

Table 7.1 *Emperor penguin diets at different locations and during different years.*

Area	Location	Year/months	Prey components (by mass)			Source
			Fish	Squid	Crustacean	
			% Principle species	% Principle species	% Principle species	
Adélie Land	Pointe Géologie	1982/Nov.	*95 Notothenids*	*3 P. glacialis*	*2 E. superba*	Offredo et al. 1985 Offredo & Ridoux 1986
Prydz Bay	ice edge	1984/Aug.-Oct.	*? P. antarcticum*		? Amphipods	[a]Green 1986
	Amanda Bay	1986/Aug.-Oct.	*97 P. antarcticum*	*3 P. glacialis*	0 Amphipods	Gales et al. 1990
Weddell Sea	Dreschler Inlet	1986/Oct.-Nov	*38 P. antarcticum*	*10 P. glacialis*	52 E superba	Klages 1989
		1990/Jan.-Feb.	*~75 P. borchgrevinki*	*A. antarcticus*	*~25 E superba*	Piatzowski & Putz 1994
		1992/Jan.-Feb.	*~75 P. antarcticum*	*K. longimana*	*~25 E superba*	Putz 1995
Mawson Coast	Auster	1988/Jul.-Nov.	*55 T. eulepidotus*	*45 P. glacialis*	[b]*E superba*	Robertson et al. 1994a
		1993/Jul.-Dec.	*32 P. antarcticum*	*31 P. glacialis*	*37 E superba*	This study
	Taylor Glacier	1988/Sep.&Dec.	*31 T. eulepidotus*	*73 A. antarcticus*	[b]*E superba*	Robertson et al. 1994a
		1993/Sep.&Nov.	*23 P. borchgrevinki*	*25 P. glacialis*	*52 E superba*	This study

[a] Green (1986) analysed scat samples (and did not attempt to quantify the diet, all other data were collected from stomach flushed birds.

[b] Robertson et al. (1994a) found trace amounts of krill only.

APPENDIX A. COMPARATIVE STRUCTURE OF THE AUSTER AND TAYLOR GLACIER EMPEROR PENGUIN COLONIES

A.1 Introduction

This appendix provides a brief description of the comparative structures of the Auster and Taylor Glacier emperor penguin colonies, and behaviours of the penguins that influence the colony structure. This information can be used to assist in the interpretation of factors in the colonies that could influence breeding success. The descriptions also enable comparisons to be made between the breeding habits of the penguins on the Mawson Coast and those elsewhere (Budd 1961, Kooyman 1993).

As mentioned in Chapter 2, Auster colony is situated on sea ice in a region of grounded icebergs 55 km east of Mawson station and 15 km offshore, where the penguins have several kilometres of open sea ice to move around. Taylor Glacier colony is 80 km west of Mawson, on a frozen lake in a 200 m long and 100 m wide valley beside the Taylor Glacier ice-tongue (Willing 1958; Chapter 1, Figure 1.2).

A.2 Colony structure during incubation

The Auster colony continually altered position throughout its period of occupation (which facilitated the regular collection of mortalities without disturbing the breeding birds; Chapter 2). During periods of strong wind >10 m/sec), the colony compacted into an area of <0.2 k^2 and progressed downwind, as birds at the windward edge of the huddle felt the cold and shuffled around the huddle's flanks to re-join the group at the leeward edge (Robertson 1990; Figure A.1). If strong winds persisted for several days, the moving colony arrived at the windward side of an iceberg where the wind was forced to rise over the iceberg forming a 10 m-broad, relatively wind-free area, and the birds formed a narrow band around the iceberg. Snow also accumulated in this area and the birds shuffled around to avoid getting buried. As strong winds abated the penguins moved away from icebergs, steadily progressing up-wind and spread out. On still days at both Auster and Taylor Glacier, the colonies expanded further, as the birds moved onto areas of fresh, clean snow, which they were often seen to eat. At both Auster and Taylor Glacier, individual males travelled up to 20 m from other birds to lie on and eat fresh snow.

Movements of the Auster colony during the winter incubation period seemed to have three motivations; 1) the hunt for fresh snow to walk on and eat; during periods of fasting, emperor penguins can dehydrate (Groscolas 1990), and probably eat fresh snow to reduce their rate of water loss; 2) a general movement away from icebergs; perhaps due to fear of their collapse (see Cameron 1969, Todd 1980); and 3) a down-wind movement in strong winds. The strong winds appear to have the primary control over colony movement during the incubation period, and if high winds persisted for several days, penguins remained close to icebergs despite being vulnerable in these positions.

A.3 Colony structure during chick rearing

At both Auster and Taylor Glacier in mid-winter, the birds packed into a single huddle, or a cluster of closely associated huddles. After hatching and during chick rearing, the colonies spread out, and tended to huddle tightly only at night or during blizzards. The July/August separation into suburbs of the winter huddling group at Auster was probably initiated by the disruption of birds trying to locate their partners, when females returned to the colony, as well as the weather warming after mid-winter. Also, parents appeared to require extra space to frequently attend and feed the chicks on their feet and often moved away from other birds to do so. This behaviour may have stimulated the fracturing of the colony.

In August/September, Taylor Glacier birds remained within a single group; after September, this group became more diffuse and was commonly separated into a series of closely associated groups, but was always confined to the 200 m long valley. By contrast, the Auster colony separated into 'suburbs' that moved independently of one another, and drifted over a large area (Figure A2). While chicks were brooded in August and September, the suburbs remained <50 m apart At this time, the parents' walking was restricted by the chicks on their feet and perhaps large huddles were still required for protection during the long nights. After emancipation of the chicks, however, some suburbs moved up to 2 km from the winter huddlmg site. Generally, this movement was along the path of parents that were journeying to and from the ice-edge. Perhaps chicks following their departing parents induced some suburbs to move seawards. The general northward movement probably was influenced by the persistent southerly winds (see Chapter 1, Figure 1.4), and maybe progression from patches of soiled to patches of clean snow. In early December, the colony comprised eight suburbs within a 6 km^2 area.

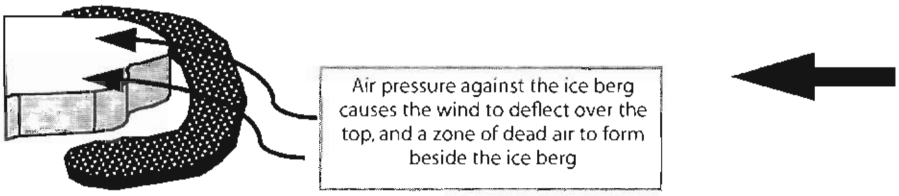
Throughout chick rearing, suburbs at Auster coalesced, split into smaller suburbs, or remained intact and discrete. There were no apparent patterns to much of this activity, although observations of the penguins' behaviour suggested a possible function of the suburbs. Through the field season, I individually marked several hundred chicks and adults, and monitored their attendance at different suburbs. Marked chicks tended to remained faithful to one suburb and most marked adults arriving at the colony walked toward the suburb where they had last attended their chicks and generally found their chick within 20 minutes. Within suburbs, parents and chicks potentially united more easily and quickly than if the colony had comprised a single group.

At Taylor Glacier, chicks may also have followed their parents seaward and extended the colony onto the sea ice. However, parents departing Taylor Glacier walked over a 5 m-high moraine which separated the valley they occupied from the sea ice. As a result of this moraine, chicks would have lost sight of their parents abruptly and were probably less inclined to follow them. No chicks were seen on the sea ice during visits to the colony in 1993 (the latest visit being 26 November).

Suburban behaviour has been observed at other emperor penguin colonies

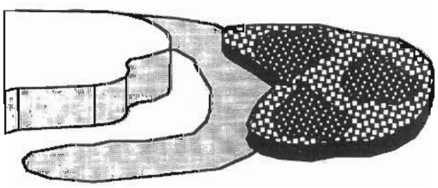
(a) Strong wind; colony in a huddle and gradually progressing downwind

(b) Strong wind continues; colony arrives at, and spreads around, an iceberg, where penguins receive shelter from the wind.

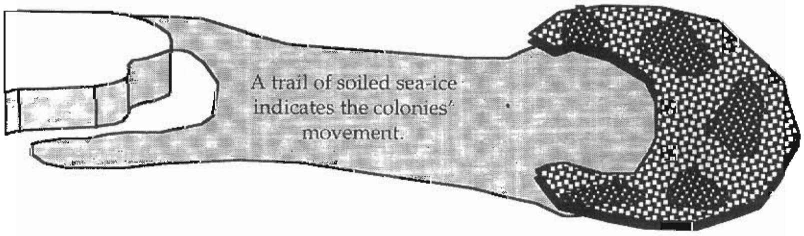


Air pressure against the ice berg causes the wind to deflect over the top, and a zone of dead air to form beside the ice berg

(c) Wind abates; colony expands and moves away from the iceberg



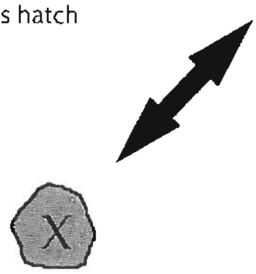
(a) Continual wind abatement; colony continues to expand in size while moving away from the iceberg and onto areas of clean snow.



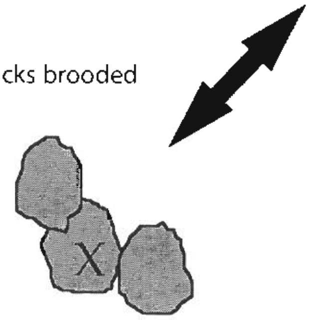
A trail of soiled sea-ice indicates the colonies' movement.

Figure A1 *Stylised diagrams of the behaviour, in response to the wind, icebergs and the requirement for clean snow, of emperor penguins during the incubation period at Auster Colony.*

(a) Late winter; chicks hatch



(b) Early Spring; chicks brooded



(c) Late spring/summer; chicks emancipated

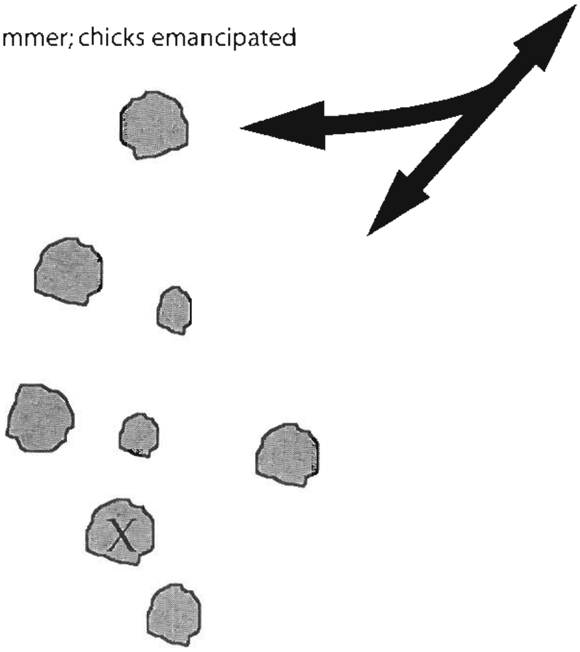


Figure A2 *Stylised diagrams of the changing structure (suburbanisation) during chick rearing, of the Auster Colony. 'X' marks the location of the colony during incubation and arrows indicate the paths of returning and departing adults*

(Hoshiai and Chujo 1976, Klages and Gerdes 1988) and probably occurs at all large colonies of this species. The fragmentation of a colony into suburbs may serve several purposes. Firstly, it may reduce the time parents spend searching for their chicks. The cacophony of sound at a single large colony might reduce the birds ability to distinguish their chick or partner's call. A second function of the suburbs is that they reduce the risk of rolling icebergs, ice-falls, or rafting sea ice (Cameron 1969, Todd 1980, Anon. 1985) from endangering the entire colony. Thirdly, the spread of the colony over a larger area diffused the guano build-up on the ice surface over a large area, which meant the birds in each suburb always were close to fresh snow to eat, and the chicks had an even, dry surface to walk over (see discussion in Chapter 2). The suburban behaviour is possible for emperor penguins because they are not territorial and the chicks are mobile and have considerable space to move around.

APPENDIX B RESEARCHER-INDUCED DISTURBANCES TO EMPEROR PENGUINS

This study of researcher-induced disturbances was opportunistic, had limited experimental controls, and was an adjunct to the main theme of the report—the foraging ecology of the emperor penguins. Therefore, it has not been incorporated into the main body of the report. Nevertheless, the study has implications for the interpretation of certain results, and contains information that may help minimise researcher impacts on penguins in future research.

B.1 Introduction

Recently, and perhaps belatedly researchers have begun to recognise the potential for certain scientific methods to inadvertently bias results and harm study animals (Ollason and Dunnet 1980, Burger 1981, Culik et al. 1990, Gales et al. 1990, Croll et al. 1991, Wilson et al. 1991, Giese 1996). A range of procedures once assumed to be benign are now thought to harm wildlife, and there are numerous examples of this from studies involving penguins (Ainley et al. 1983, Culik et al. 1993, Giese 1996). This study reports on the impacts on emperor penguins of certain scientific procedures that were necessary to quantify the birds' foraging ecology. In particular, this study aimed to assess the effects on foraging performance and breeding success of: 1) the attachment and carrying of external instruments, 2) stomach flushing, and feeding following stomach flushing, and 3) handling for foraging energetics determinations. Each of these manipulations had the potential to reduce the penguins' foraging performance and chick raising ability, but to date no published reports have assessed the effects of these types of investigator disturbance on emperor penguins.

The attachment of instruments to birds can influence their locomotive ability because birds rely on having a streamlined body shape to minimise turbulence through air or water (Obrecht et al. 1988). Penguins have one of the most hydrodynamic shapes of any known object (Hui 1988, Oehme and Bannasch 1989, Bannasch 1995), and instruments attached to them can increase their energetic costs (Culik and Wilson 1991), alter their foraging behaviour (Gales et al. 1990, Croll et al. 1991), and even reduce their breeding success (Watanuki et al. 1992, Croll et al. 1996).

Current assessments of the diet of penguins invariably involve stomach-flushing the birds (Wilson 1984). While this technique is effective and more humane than killing birds (Duffy and Jackson 1986, Ryan and Jackson 1986, Gales 1987), the procedure is invasive, and its impacts on penguins are rarely investigated (for exceptions, see Clarke and Kerry 1994, Robertson et al. 1994b). One obvious detrimental effect of stomach-flushing a parent penguin is that its chick is deprived of a meal. Supplemental feeding of the parent after removing its stomach contents might negate this meal loss for the chick. This was trialed in this study, to see if it could improve the breeding success of stomach-flushed parents.

Simply handling penguins can elevate their heart rates (Culik et al. 1990, Giese 1995) and body temperatures (Boyd and Sladen 1971), yet handling is necessary for most procedures in penguin research, including the energetics determinations undertaken during the current study (see Chapter 4 and 5). The multiple handling and blood sampling required for energetics determinations are likely to stress the birds considerably, and may affect their breeding success. A final aim of this study, therefore, was to investigate the breeding success of emperors that had been manipulated for foraging energetics determinations.

B.2 Methods

B.2.1 General

The specific techniques of this study are described in full in Chapters 4 and 5, so are only briefly summarised here. To capture penguins, I positioned myself 1 km seaward of the colony on the line of penguins commuting between the colony and the ice-edge. Penguins were intercepted as they passed, which involved a 5–20 second chase. They were restrained in a cone-shaped canvas bag (Robertson 1991), hooded to reduce their anxiety (Kosiorek and van den Hoff 1994), weighed (± 0.1 kg) using a spring balance, and processed as needed for the various aspects of the study (see below). Penguins were marked on the chest with 'Nyanzol' dye and released in their direction of travel.

The attendance patterns of the manipulated birds were recorded in near-daily searches of the colony. These data were then examined to predict the birds' ability to raise a chick to pre-fledging age (until early December). Birds that frequented the colony regularly, and were standing beside or feeding a chick when resighted, were deemed to have successfully raised a chick. Birds that were resighted less than twice, or remained at the colony for >5 days without being seen attending a chick, were considered to be failed breeders. All other birds, for whom no definitive information on their ability to raise a chick was recorded, were classed as 'unknown'. I compared the abilities to raise chicks of handled birds with the overall breeding success at the colony (see Chapter 2).

This method of predicting breeding success was practical only for penguins that were caught between August and October. The dye applied to penguins prior to August faded, making it impossible to recognise individual birds, and the breeding success of many penguins handled after October was difficult to predict, since thereafter the birds visited the colony only briefly (<1 day) and could have eluded detection.

B.2.2 Effects of instruments

Penguins were fitted with instruments as they departed the colony. On their return to the colony, the penguins were recaught, weighed, had the instrument removed, and were released. The birds were held for <60 sec during each capture. I assessed the effects of carrying different sized instruments on the foraging performance of females in winter and of birds of both sex in spring. In addition, I investigated the effect on breeding success of carrying a 100 g instrument (a time-depth-recorder, TDR) for a single 10–25 days foraging trip in August, September or October, by comparing the breeding success of these instrumented birds with the overall breeding success at the colony.

Shape & size	Time-depth recorder (TDR)	Time-depth-speed recorder (Paddle)	Satellite tracker (PTT)
Lateral profile			
Dorsal profile			
Frontal profile			
Dimensions	11 x 4 x 1 cm	11 x 4 x 2 cm	11 x 7 x 2 cm (+ 20 cm antenna)
Frontal surface area (FSA)	4 cm^2	8 cm^2	14 cm^2
Unit FSA as % of penguin FSA	0.7 %	1.4 %	2.4 %
Mass	100 g	250 g	450 g
Mass as a % of the mass of a 28 kg penguin	0.4 %	0.9 %	1.6 %

[a] Arrow indicates a protrusion in the instruments housing where a worm-clamp was secured during attachment of the instrument to the penguin's back.

Figure B1 *A comparison of the shapes and sizes of instruments deployed on the backs of emperor penguins from Auster Colony to record the penguin's foraging behaviour.*

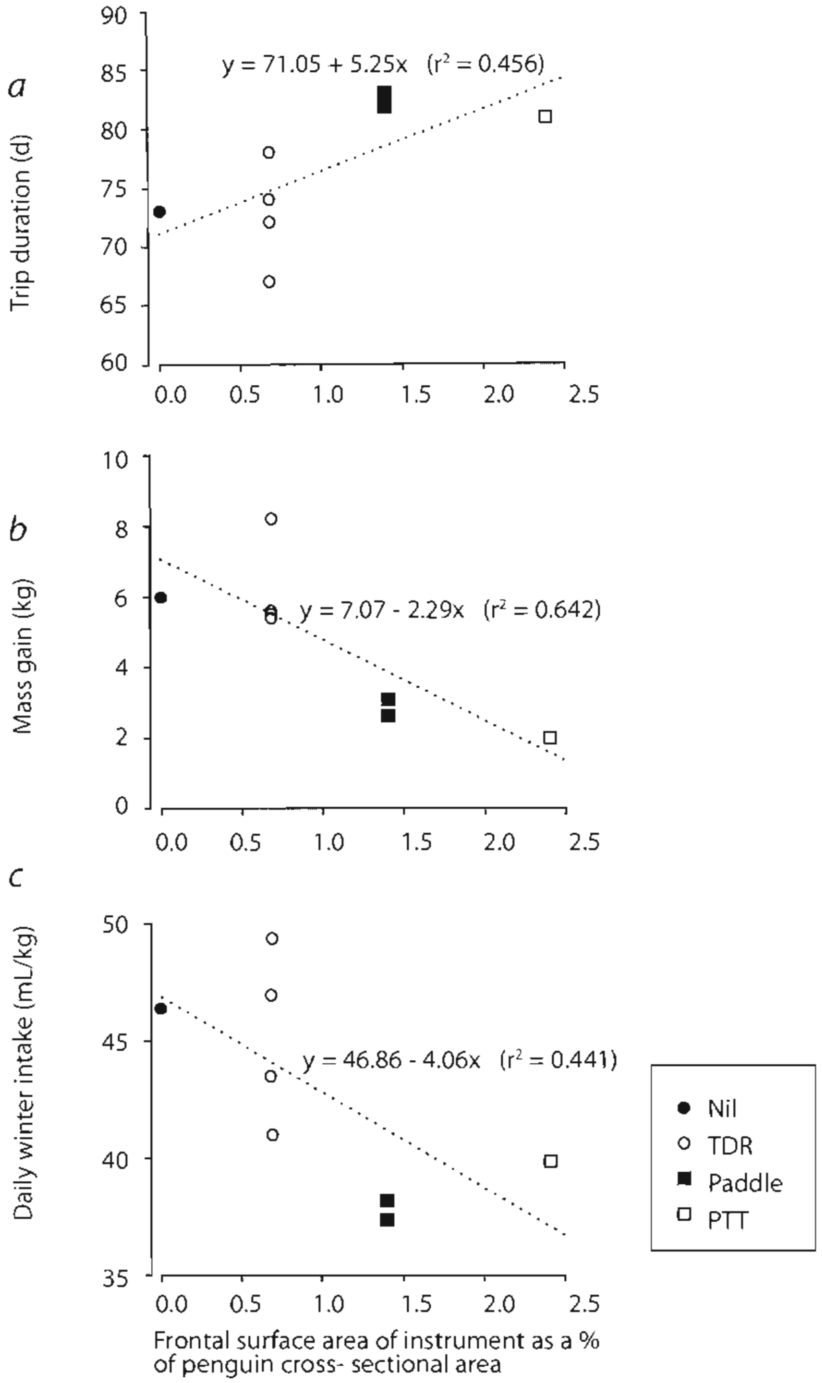


Figure B2 *Regressions of emperor penguin (a) foraging trip durations (b) mass gains during trips (c), and daily water intake against the frontal surface area as a percentage of penguin cross-sectional area, of instruments attached to female penguins foraging in winter.*

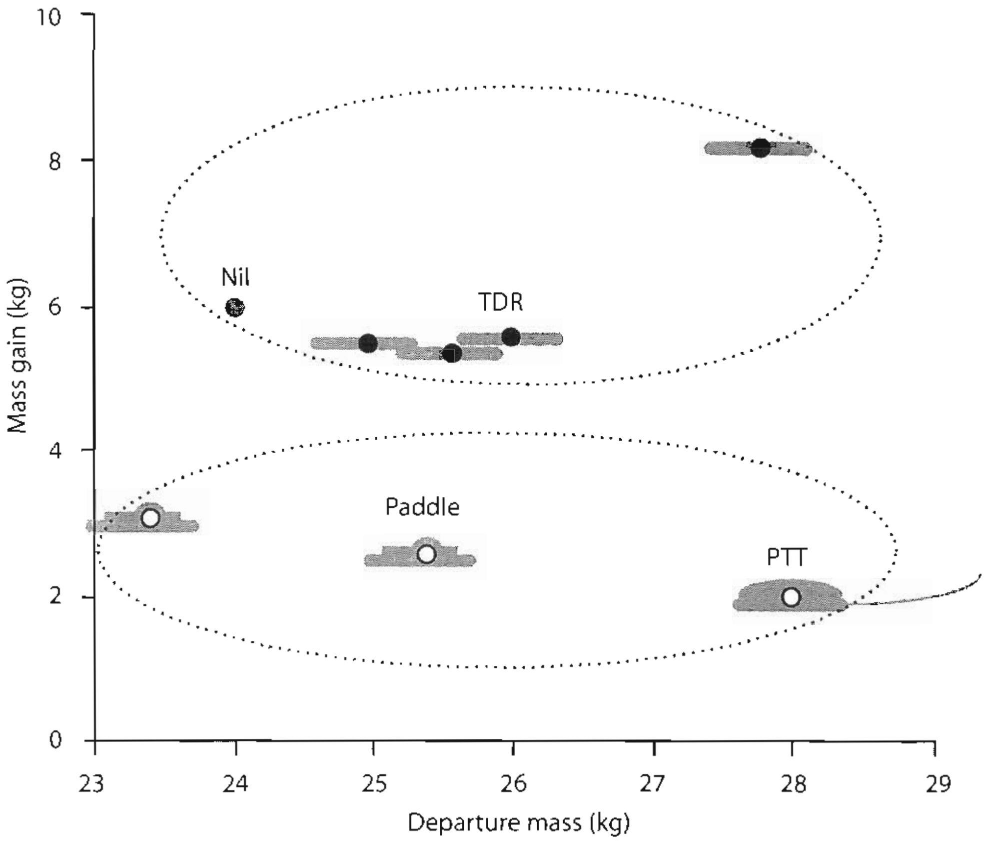


Figure B3 *Body mass gained by female emperor penguins during winter foraging trips, against body mass when departing the colony prior to the trip. The type of instrument (see Figure B1) attached to each penguin is depicted. The two dotted ovals draw attention to an apparent similarity in mass gain by the unencumbered penguin and those that carried TDRs, and by the PTT bearing penguin and those that carried paddles, as well as a distinction between the two groups.*

To assess the effects of carrying instruments of different sizes on foraging performance in winter, I compared the trip durations, mass changes, and water turnover rates (an indication of prey consumption rates; Nagy and Costa 1980), of female emperors during their winter foraging trips. Three types of instruments were attached to these females: TDRs, time-depth-speed recorders (Paddles), and satellite tracking devices (PTTs); the sizes of these devices are compared in Figure B1. Initial sample sizes for this study were 16 TDR, three Paddle, three PTT, and 10 unencumbered birds (i.e. controls). The short day-lengths in winter, when the females often returned during night-time, made it difficult to sight and recapture the birds before they had entered the colony. The final sample size, therefore, was reduced to four TDR, two Paddle, one PTT, and one unencumbered bird/s. Regressions were performed to assess the relationships between the frontal surface area of the instruments, as a percentage of penguin cross-sectional area, and the penguins' foraging performance indicators. The slopes of the regressions were tested using ANOVAs to see if they were significantly different from zero.

During spring, when the effect of instrument size on foraging performance was assessed again, the penguins were returning to emancipated rather than newly hatched chicks and trip durations were shorter than they were in winter (10–25 days compared with >60 d). In spring, 18 penguins were fitted with TDRs and 4 with Paddles. The pre-departure masses, mass gains during foraging trips and trip durations of penguins bearing the different sized instruments were compared using t-tests.

B.1.3 Stomach flushing and supplemental feeding

Penguins were stomach-flushed as they returned to the colony. To flush their stomachs, birds were restrained, had a plastic 'lavacuator' tube inserted into their oesophagus and their stomachs were filled with warmed seawater until they regurgitated. The process was repeated until no more stomach contents could be obtained, or to a maximum of five flushes. The birds were then released. During flushing, each penguin was held for 5–15 min. The numbers of penguins flushed were 17, 23, 14 and 26 in July, August, September and October, respectively. In July the birds were females returning from their winter foraging trips, in August they were males returning from their first foraging trip after their winter fast, and in September and October the birds were of both sexes. The breeding successes of these penguins were compared with the overall breeding success at the colony.

In both July and August, five of the flushed penguins were fed 1.5–2.0 kg of homogenised antarctic silverfish (*Pleuragramma antarcticum*) a common prey of emperor penguins (Gales et al. 1990, Robertson et al. 1994a, and Chapters 4 and 5). The antarctic silverfish had been caught by trawling on the Mawson Coast in January 1993, and snap-frozen until required. Immediately prior to flushing a penguin that was selected (at random) to be fed, I defrosted and homogenised 2 kg of the fish. The homogenate was spooned into a pastry-bag fitted with a 30 cm-long plastic tube (1 cm internal diameter, 1.3 cm external diameter) and kept warm (25°C). Immediately after flushing the penguin, the plastic tube was carefully inserted into the birds' oesophagus and by gradually squeezing the pastry-bag, the homogenised fish was ejected directly into the penguin's stomach. Feeding a bird in this manner took 2–5 min.

B2.2 Energetics determinations

Birds selected for energetics determinations were caught as they departed the colony. They were injected in the pectoral muscle with 1.0 mL of water containing tritium isotope and released into an open pen (4–8 m^2) on the sea ice for a two hour isotope equilibration period. Following equilibration, the penguins were restrained, had a 2 mL blood sample drawn from their radial vein, and were released. When the penguins returned to the colony, they were recaught, weighed, had a 2 mL blood sample drawn from their radial vein and were released. These penguins were restrained for approximately 2 minutes on each occasion that they were held (i.e. before and after the two hour isotope equilibration period and on return to the colony).

The breeding success of penguins that were handled for energetics determinations during August, September and October, were compared with the overall breeding success at the colony.

B.3 Results

B.3.1 Effects of instruments

During their two-month foraging trips in winter, females that carried larger external instruments (PTTs and paddles) tended to have longer trip durations, gain less body mass and had lower water intakes, indicating lower rates of prey consumption, than the unencumbered females or those that carried smaller devices (TDRs; r^2 = 0.456, 0.642 and 0.441, respectively; Figure A2.3). The trend was statistically significant for mass gain against instrument size (ANOVA: $F_{1,6}$ = 9.121, p = 0.023) but not for trip duration or water intake per day against instrument size (ANOVAs: $F_{1,6}$ = 5.009, p = 0.067, and $F_{1,6}$ = 4.741, p = 0.072, respectively, the percentage data were transformed by arcsine $\sqrt{[x+1]}$ to homogenise the variances and scale zeros into the positive range). Given the significant relationship between mass gain and instrument size, the result for water intake and instrument size is surprising, and presumably reflects the small number of penguins sampled. During their foraging trips, the unencumbered penguin and those that carried TDRs gained comparable masses, and the PTT and paddle-bearing penguins gained similar masses.

During September and October, penguins fitted with TDRs and paddles were similar in body mass (23.8 kg and 23.3 kg, respectively; Figure B3). While on foraging trips, penguins carrying the different sized instruments gained comparable body masses (3.2 kg and 4.4 kg, for TDR and paddle-bearing birds, respectively) and were away from the colony for similar trip durations (19.9 days and 18.5 d, respectively; Figure B3). This suggests that during the 2–3 week foraging trip in spring, the larger paddles did not affect the penguins' foraging ability more than the smaller TDRs did, which contrasts with the apparently different effects of these instruments on females foraging for >8 week in winter.

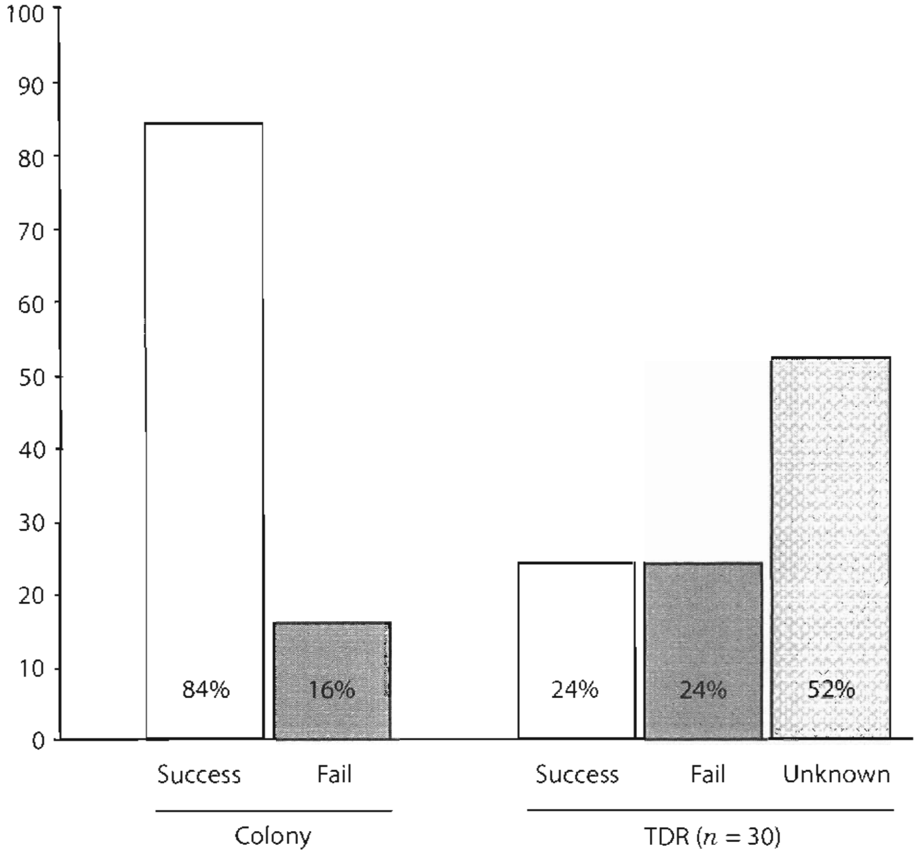


***Figure B4** The ability of emperor penguins from Auster Colony to raise a chick to pre fledgling age (breeding success) following manipulations to attach and remove a TDR, and carrying the TDR for one 10 to 25 day foraging trip during spring, compared with the overall breedinng success at the colony that contained 13,300 breeding pairs (from Chapter 2).*

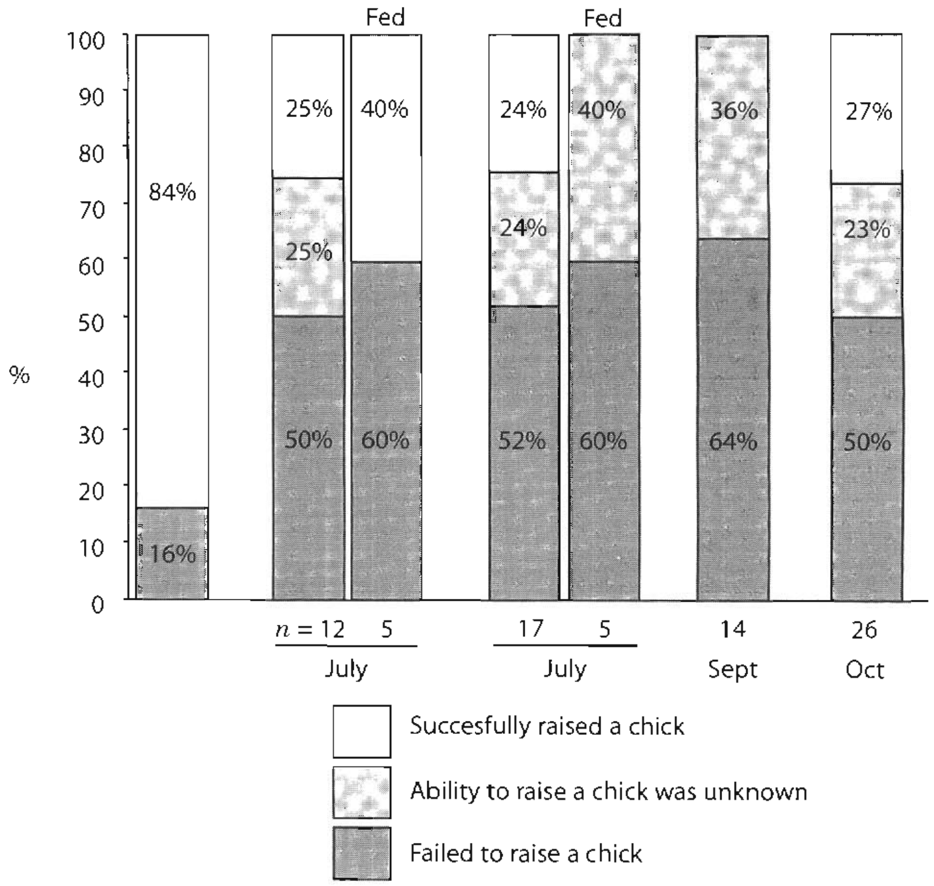


Figure B5 *A comparison of the breeding success of emperor penguins that were stomach flushed and those that were stomach flushed then fed a 1.5-2.0 kg meal of homogenised antarctic silver fish,* Pleuragramma antarcticum, *between July and October, and the overall breeding success at the colony (from Chapter 2).*

Table B1 *Statistical comparisons (t-tests) between penguins that carried TDRs and those that carried paddles during foraging trips in September and October. Comparisons are of pre-departure body masses, mass gains and trip durations.*

Device	n	Departure mass		Mass gain		Trip duration	
		(kg)	± 1 SD	(kg)	± 1 SD	(d)	± 1 SD
TDR	18	23.8	1.3	3.2	1.5	19.9	5.8
Paddle	4	23.3	1.9	4.4	1.3	18.5	2.4
t			0.680		1.533		0.480
df			20		20		20
P			0.504		0.141		0.637

Of 29 penguins that carried TDRs for one foraging trip during August, September or October, seven (24%) failed to raise chicks and seven did raise chicks; the breeding success of 15 penguins (52%) was unknown (Figure B4). This compared with the overall rate at the colony during 1993 of 84% success and 16% failure (see Chapter 2). Therefore, carrying a TDR for one foraging trip, plus the handling associated with the attachment and removal of the TDR, appeared to have a detrimental effect on a penguin's breeding success.

B.3.2 Stomach flushing and supplemental feeding

There were no significant differences in the body masses, the number of flushes received, or the dry mass of the stomach contents removed, between the flushed-only and the flushed-and-fed birds (separate analysis for females and males; Table B2a–b). Within each sex, therefore, flushed-only and flushed-and-fed penguins were assumed to be comparable, with the only difference between them being that of feeding.

From the group of 12 flushed-only females, six failed to raise chicks, three were unknown and three raised chicks (Figure B5). Of the five flushed-and-fed females, three failed and two successfully raised chicks (Figure B5). From the group of 17 flushed-only males, nine failed, four were unknown and four successfully raised chicks. Of the five flushed-and-fed males, three failed to raise chicks and two were unknown. These results suggest the supplemental feeding did not improve the chick raising ability of the stomach-flushed emperor penguins, and, if anything, feeding had a slightly detrimental effect on the penguins' ability to rear a chick.

Penguins that were stomach-flushed during July, August or October had a 50–75% chance of failing to raise a chick, considerably higher than the overall failure of 16% of breeders at the colony (Figure B5). If stomach-flushed during September, the penguins appeared to be even more susceptible to interference with a 64–100% chance of failure (Figure B5).

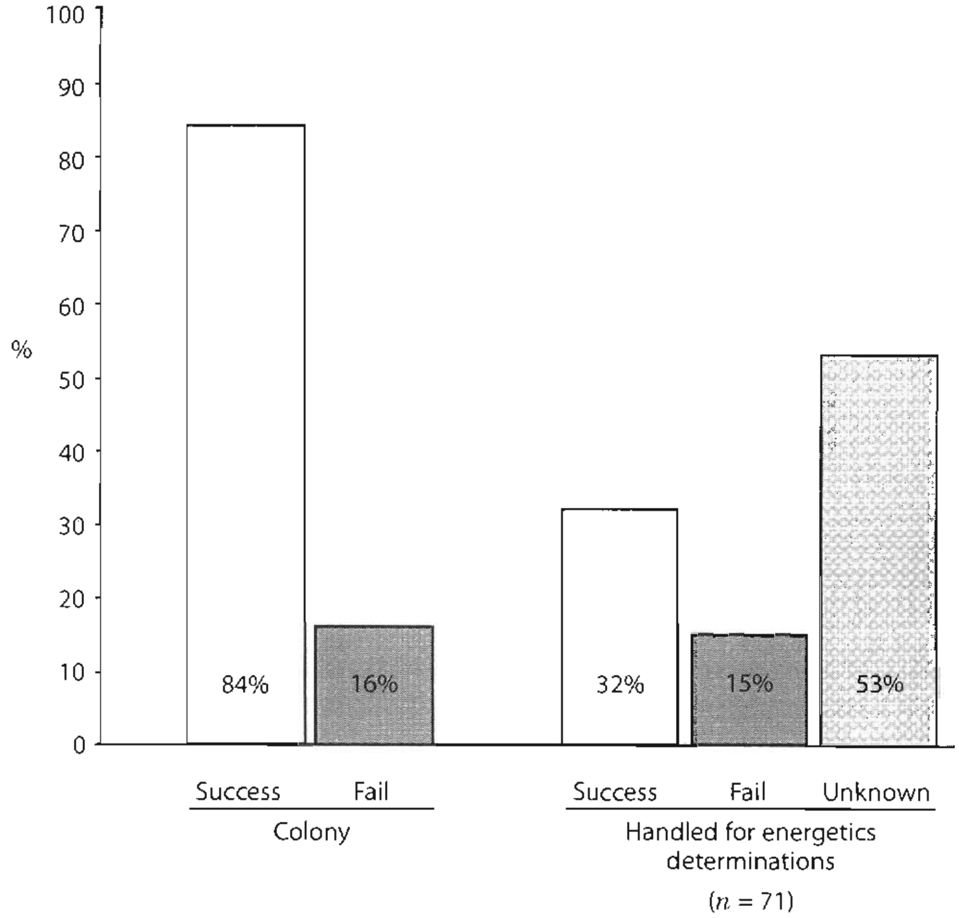


Figure B6 *The ability of emperor penguins from Auster Colony to raise a chick to pre-fledgling age (breeding success) following manipulations for foraging energetics determinations during spring, compared to with the overall breeding success at the colony that contained 13,300 breeding pairs (from Chapter 2).*

***Table B2** Statistical comparisons (t-tests) between emperor penguins that were stomach flushed only and stomach flushed then fed. Comparisons are of arrival body masses, number of flushes and dry masses of contents obtained.*

a) Females arriving at Auster in July.

Disturbance	n	Arrival mass		Flushes		Dry mass of stomach contents	
		(kg)	± 1 SD	(n)	± 1 SD	(g)	± 1 SD
Flushed only	12	31.5	2.9	2.8	1.1	228.9	112.2
Flushed + fed	5	32.3	5.6	3.0	0.7	191.2	57.2
t			0.832		0.306		0.704
df			15		15		15
P			0.419		0.764		0.539

b) Males arriving at Auster in August.

Disturbance	n	Arrival mass		Flushes		Dry mass of stomach contents	
		(kg)	± 1 SD	(n)	± 1 SD	(g)	± 1 SD
Flushed only	17	29.9	2.0	2.8	0.7	344.6	146.0
Flushed + fed	5	29.1	1.5	2.4	0.5	272.2	56.3
t			0.852		1.116		1.071
df			20		20		20
P			0.405		0.278		0.297

B.3.3 Handling for energetics determinations

Of 71 penguins handled for energetics determinations, 11 (15%) failed and 23 (32%) were successful at raising chicks. The ability to raise chicks of 37 (53%) penguins was unknown (Figure B6). When compared with the overall colony rates of 16% failed and 84% successful, these results suggest that performing energetics determinations on the emperor penguins is likely to have reduced the birds' breeding success.

B.4 Discussion

B.4.1 Effects of instruments

Compared with other penguins, emperors have large body sizes (>25 kg body mass), and because of this, the instruments I attached to them were relatively small (0.7–2.4% of the emperors' cross-sectional area and equivalent to 0.4–1.6% of the birds' body mass). The frontal surface area (FSA) of external instruments attached to other penguins in recent studies have ranged from 2–5% of the cross-sectional area of the penguins, and have been equivalent to 1–5% of the penguins' body mass (e.g. Davis and Miller 1990, 1992 Williams et al. 1992b, Bengtson et al. 1993, Croxall et al. 1993, Wilson et al. 1995, Davis et al. 1996, in studies of

Adélie [*Pygoscelis adeliae*], gentoo [*P. papua*], chinstrap [*P. antarctica*], macaroni [*Eudyptes chrysolophus*], and Magellanic [*Spheniscus magellanicus*] penguins).

Despite the relatively small size of the instruments in the present study, they still appeared to influence the foraging ability of female emperor penguins during their >60 day winter foraging trips. A reduction in body mass gained and an increase in trip duration was evident in females that carried instruments with FSAs >1% of the penguins' cross-sectional area. These effects were slight however, and comparable effects were not apparent on birds conducting 2 to 3 week foraging trips in September and October. Perhaps the shorter foraging trips by penguins in September and October were insufficient for the effects of instrument size to become evident. Alternatively, the small sample sizes of this study may conceal the effects of device size, since small sample sizes are likely to detect only gross effects (Cohen 1977). A third possibility is that the difference between the effects of instruments on females in winter and on birds of both sex in September and October was related to the penguins' reproductive stages, these being incubation and brooding and/or early crèche, respectively. Adélie penguins apparently are more affected by devices attached to them during incubation stages than during post-hatching (Clarke and Kerry 1994), and emperor penguins may respond similarly.

Penguins rely on their body shape to minimise turbulence through water and instruments attached to them can increase this turbulence and subsequently increase energetic costs of swimming (Culik and Wilson 1991, Bannasch 1995). In attempts to negate the interference caused by external devices, implanted devices have been tested on penguins. However, these devices require surgery, extended handling times and may still result in increased energetic costs due to the discomfort they may cause the birds (Culik and Wilson 1991). External instruments on penguins are simple to deploy and retrieve, and important criteria that minimise their effects have now been recognised. For example, the instruments should be similar in colour to the penguin (Wilson et al. 1990), be placed on the lower half of the bird's back, where they do not interrupt laminar water-flow across the back, be streamlined in shape, and have a minimum FSA (Culik et al. 1994, Bannasch et al. 1994). Although the penguins may attempt to 'preen off' any external device (e.g. Wilson and Wilson 1989), if the units are sufficiently small and well placed or they should not significantly alter the foraging behaviour of their incumbent penguin, particularly during short (<25 days) foraging trips.

Results of the present study suggest that the FSA of a device attached to an emperor penguin needs to be <1% of the cross-sectional area of the penguin before effects of the device on foraging ability may become negligible. Similarly, royal penguins (*Eudyptes schlegeli*) can be impaired by back-mounted instruments that have FSA's that are 2.3% of the penguins' cross-sectional area, but not by instruments that have FSA's that are 0.24% of the penguins cross sectional area (Hull 1997). With current trends toward increased miniaturisation of instruments, it is possible that in the future all devices attached to penguins will be smaller than these critical sizes.

B.4.2 Stomach flushing and supplemental feeding

Stomach flushing an emperor penguin severely reduced its ability to raise a chick, and during September, when the rate of chick mortality peaked (Chapter 2), the penguins appeared to be particularly susceptible to breeding failure following stomach flushing. In Adélie penguins, stomach flushing apparently does not reduce breeding success (Clarke and Kerry 1994, Robertson et al. 1994b). Amongst penguins, emperors may be particularly susceptible to disturbance from manipulations, or alternatively, Adélie penguins are particularly tolerant of stomach flushing.

Feeding did not significantly increase the abilities of stomach-flushed emperor penguins' to raise chicks. Although feeding provided the birds with food that they could pass on to their chicks, it also subjected the birds to longer handling times and the additional trauma of having an artificial meal injected into their stomachs. The present study was opportunistic and was conducted in less than ideal conditions. For instance, the equipment was adapted rather than designed for force-feeding procedures, and ambient temperatures of –25°C hampered the studies efficiency. The negative result, therefore, should not preclude attempts by other researchers to feed penguins after removing contents from their stomachs, particularly species which may be more tolerant of handling than the emperors.

During analysis of the stomach contents, I regularly found portions of penguin stomach lining, which had presumably been lifted from the stomach wall during the flushing process. The appearance of stomach lining in samples flushed from penguins is concerning and has not previously been reported. Emperor penguins may readily shed their stomach lining in the course of regurgitating meals to their chicks, or, alternatively, the occurrence of stomach lining may signal physical damage caused by the stomach-flushing procedure. This finding highlights the need to better understand the digestive tract and food delivery system of emperor penguins.

Although stomach-flushing penguins is an effective means of assessing their diet, and more humane than killing birds (Duffy and Jackson 1986, Ryan and Jackson 1986, Gales 1987), there is considerable social pressure from co-workers and the public against the continued stomach-flushing of penguins. A need exists to better understand and reduce the harmful consequences of the procedure and to investigate alternative, less invasive, techniques for assessing penguin diet.

B.4.3 Handling penguins

All three forms of scientific manipulation assessed in this study; attachment of devices, stomach-flushing, and energetics determinations, reduced the breeding success of emperor pengnins. Furthermore, the negative effects may have been greater than those recognised because chick size was not investigated, and it is possible that even successful penguins raised under-sized chicks that had less than average chances of first-year survival.

Amongst penguins, emperors may be particularly susceptible to disturbance from manipulations. In contrast with other penguins, emperors are probably exposed to less aggressive behaviour because they do not defend territories and have no land predators during most of their breeding period. Being less exposed to aggressive behaviour may enhance the emperors susceptibility to disturbance from human contact.

An observation from the present study raised the question—do emperor penguins that are handled retain a long term association of humans representing a threat? In 1988, aluminium flipper-bands, used to attach instruments and for energetics determinations, were attached temporarily to Auster emperor penguins (Robertson 1994). Not all the birds were recaptured in 1988, so during the present study 24 of these band-bearing birds were recaught and had their bands removed. When approached, the banded penguins deviated in a 50–100 metre arc around the human and apparently panicked if the human continued to approach. This behaviour contrasted with the behaviour of penguins that had not previously been handled—when approached by a human, these birds would continue with caution but minimal deviation. Despite it being five years since their only previous close encounter with a human, the banded penguins apparently recognised the human as a threat and attempted to avoid close contact.

Different birds have different reactions to being handled therefore there is a need for researchers to recognise the nuances of their study species in order to reduce the impact on their study animals and minimise potential biases in their results. Emperor penguins are affected by human manipulation and when researching them, efforts should be made to minimise their stress, handling times and the number of birds handled.

B.5 Conclusion

Researchers can influence the behaviour, reproductive success and survival of their study animals potentially leading to biased observations and a detrimental impact on wild populations (Giese 1995, and references therein). Any research that involves the handling of wildlife must balance the disruption caused to the few handled animals against the scientific, economic and conservation benefits of the research to the population, species or ecosystem in which the individuals operate. It is prudent, in terms of animal welfare and scientific rigour, that any researcher who manipulates animals recognises and quantifies the possible effects of their procedures, and disseminates this information to reduce the disturbances and biases of future studies.

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