Breeding biology and feeding ecology of little penguins at Phillip Island – a basis for a monitoring program
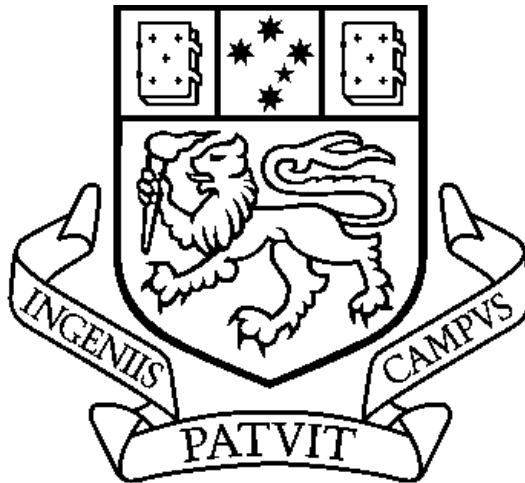
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Breeding biology and feeding ecology of little penguins *Eudyptula mino*r at Phillip Island – a basis for a monitoring program

by

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Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

INGENIIS CAMPVS PATVIT

University of Tasmania

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DECLARATION

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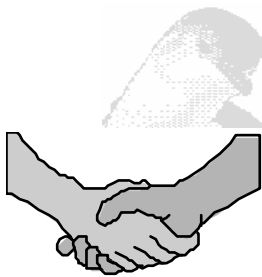
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Acknowledgments

ABSTRACT

This research examined the breeding performance of little penguins (*Eudyptula minor*) at Phillip Island in south east Australia. A major goal was to relate breeding success to fluctuations in food availability within and between seasons. Data was collected on nest attendance patterns, pair bonding, chick growth rates, chick meal mass, adult time budget and diet. Sampling extended over two reproductive seasons, one with good and other with poor reproductive success.

Implanted identification transponders combined with an automated penguin monitoring system were used to determine daily nest attendance. Successful breeders had shorter incubation shifts and undertook more foraging trips than failed breeders during both incubation and chick guard periods. The later a little penguin started to breed the poorer was its breeding performance.

Males guarded their partners throughout the pre-egg periods but left their females as soon as the first egg was laid. Observations of the penguin pairs in their burrows showed that they had different partners on 33% of the recorded occasions. This was used as an indication of extra-pair copulation during the pre-egg period. Changing partners and burrows between seasons decreased reproductive success. Inter-seasonal divorce rate was 28%, one of the highest amongst penguins, even though evidence suggests that divorce behaviour has no obvious benefit for little penguins.

During chick rearing, four fish species comprised 93% of the penguins' diet. These species were red cod *Pseudophycis bachus*, barracouta *Thyrsites atun*, warehou *Seriolella brama* and anchovy *Engraulis australis*. Mean meal mass decreased as the breeding season progressed while foraging trip duration increased. Birds kept the length of their foraging trips below two days during the good season. During the bad season birds foraged longer than two days right from the beginning of the post guard. Compared with successful breeders from the bad season, successful breeders from the good season guarded their chicks for 6 days longer, had a post-guard that was 9 days shorter and their chicks grew faster.

Little penguins exhibited substantial temporal and seasonal variation in their time budget and foraging performance. The variation was used to identify whether differences in breeding performance and food availability were related to natural causes or to commercial fishing activities. As the stock biomass is unknown for most of the commercial fishery in Victorian waters, it is difficult to prove the existence of detrimental effects of fishery on the food supply for the penguins. There was evidence, however, that fishery may impact on the penguin foraging performance. The little penguins from Phillip Island consumed almost the same amount of fish as was caught by commercial fisheries in Victoria. Pilchards and anchovies have decreased dramatically in importance in the penguin diet while the commercial catches of these fish have increased progressively. This suggests that there might be competition between penguin feeding and commercial fishing.

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1   Thesis introduction

The little penguin *Eudyptula minor* is the smallest of the penguins. It is endemic to southern Australia and New Zealand (Marchant and Higgins 1990). Many factors affect the little penguins' life cycle and their breeding performance. Long term studies, i.e. repeated surveys using standardized methods, have revealed aspects of little penguin biology and their ecology which have been used in many situations as a case study for the *Sphenicidae* family (Reilly and Cullen 1981; Dann and Cullen 1990; Dann 1992; Dann et al. 1995; see also Williams 1995). The mortality of the little penguin is one of the highest amongst penguins (Williams 1995). At Phillip Island, Dann (1992) determined that 80% of mortality on land was caused by introduced species, foxes *Vulpes vulpes* and dogs *Canis familaris*, and road kills. In the 1980s, these causes resulted in a decrease in the breeding population to low levels. Further conservation measures were taken and the population at Phillip Island seems now to be stable (Ellis et al. 1998). The world population of little penguins has declined only slightly in the past one hundred years and it is the only penguin species outside the Antarctic region classified as lower risk (not threatened) on the IUCN Red List (Ellis et al. 1998).

Lack of food seems to be a major threat to the little penguin population since starvation is likely to be the major cause of adult mortality at sea (Dann 1992; Harrigan 1992; Hobday 1992). Many factors limit the availability of prey to the predator including prey density, environmental conditions and competition with commercial fisheries (Furness and Ainley 1984; Boersma 1987; Croxall et al. 1988; Croxall 1989; Furness and Barrett 1991b; Boersma and Stokes 1995). Little penguins prey upon several species which are harvested commercially but the abundance of these fish stocks is unknown which makes it difficult to determine the relationship between commercial fishing and penguin feeding in the foraging zone of the Phillip Island population (Montague and Cullen 1988; Cullen et al. 1992; Kailola et al. 1993; Neira et al. 1997). However, there is evidence that a successful penguin breeding season at Phillip Island, Victoria depends on the availability of pilchards and anchovies, which constitute about 42% of the little penguin diet (Montague and Cullen 1988; Cullen et al. 1992; Hobday 1992; Norman et al. 1992; Norman et al. 1996).

The present study was initiated as a first step in assessing the use of the little penguin as an indicator in a monitoring program to examine changes in the availability of prey in

the marine ecosystem around Phillip Island. Food supply provides a major selective force determining the breeding season and low abundance of food will have a negative effect on breeding success in seabirds (Ashmole 1971). Previous studies on breeding and foraging ecology of little penguins have dealt with population averages and variations between seasons (Kinsky 1960; Reilly and Balmford 1975; Reilly and Cullen 1981; Thoday 1982; Reilly and Cullen 1983; Dann 1992; Weavers 1992; Fortescue 1995). Breeding performance was usually measured as the number of chicks fledged per pair per season. This variable is useful to compare seasons but provides little information on factors affecting breeding performance during the season (Croxall et al. 1988). It is crucial to determine variations in the breeding performance in a season to understand the factors causing intra-seasonal fluctuations of food availability (Wooller et al. 1992). The difficulties in working with burrow-nesting penguins using manual methods have not allowed finely detailed studies on little penguins. Temporal changes within a season may cause high variability amongst individuals which make it difficult to detect intra-seasonal fluctuations in previous investigations. As a different approach was needed to determine which variables are sensitive to intra-seasonal fluctuations of food availability, this study was designed to provide on a daily basis, fine detail of the breeding and foraging ecology of individual little penguins.

1.1 The use of seabirds to monitor prey availability

It is well recognized that fisheries have a large impact on marine ecosystems. Depletion of higher trophic commercial targets, like herring and mackerel stocks in the North Atlantic, has pushed fisheries to move toward new stocks at lower trophic levels, like sandeels and anchovies, which increases pressure on top predators, in particular marine mammals and seabirds (Sherman et al. 1981; Furness and Ainley 1984). Calculations of the primary production required (PPR) to sustain fisheries revealed high values for continental shelves (24.2 to 35.3%) and upwelling systems (25.1%) where most of commercial fish are caught (Pauly and Christensen 1995). These values leave little room to increase the annual world wide fish catch of 94 million tonnes, which also includes an impressive by-catch of 27 million tonnes per year (Pauly and Christensen 1995). In economic terms, the world fishing fleet has annual losses of around US$ 54 billion and a further estimated cost of US$ 25 billion each year caused by poor fishery management (Beddington 1995). It has been suggested therefore that any improvement

in the fishery catch will come through better management (Lavigne 1992; Pauly and Christensen 1995).

Forecasting catch limits or detecting signs of over-exploitation are difficult tasks when conventional assessment methods, based on catch statistics, are used or when fishery management is considered in the context of a single population of fish (Butterworth 1980 in Crawford et al. 1983; Shelton 1992). Fishery biologists are considering ways to incorporate interactions such as predator-prey relationships into practical fishery management.

There has been a unique approach to fishery management in the Antarctic region. The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) requires that the management of any Antarctic fishery should take into account a conservation standard, i.e. that the exploitation of resources should not adversely affect natural consumers (CCAMLR 1982). CCAMLR, through its Ecosystem Monitoring Program (CEMP), selected both the predator species and the standard methods thought to be best suited to exercise this management (CCAMLR 1991). CCAMLR is trying to determine whether the fishing of krill *Euphausiacea*, the main prey for vertebrate consumers in the Antarctic food web, is having or is likely to have any impact on the ecosystem (CCAMLR 1982). Although there has been a very large harvest of krill, *Euphausia superba*, its current fishing is not considered a threat to the balance of the Antarctic ecosystem (Croxall et al. 1992a; Pauly and Christensen 1995).

In Australia, fishery management has been based on catch statistics (Kailola et al. 1993) which may not be sensitive enough to detect signs of collapse in fish stocks (e.g. Butterworth 1980 in Crawford et al. 1983). Australian waters are characterized by a low concentration of nutrients which do not sustain a highly productive fishery compared with other fishery regions in the world. There are indications that most commercial fishery resources are fully exploited or over-fished (Fishery Status Reports 1997).

In Victoria, for instance, few studies have been done on the population dynamics of commercial fish and the abundance of its stocks is mostly unknown (Hobday 1992; Kailola et al. 1993). There, the main fishery is concentrated on species from the lower levels of the food web, mainly pilchard, *Sardinops sagax* and anchovy, *Engraulis australis* (Neira et al. 1997). Apart from little penguins, the marine ecosystem of Victoria also sustains other seabird and marine mammal populations (e.g. Norman 1992;

Norman et al. 1996). Pilchards and anchovies represent about 72% of the catch by weight in the region which mainly supplies a growing pet food industry (Neira et al. 1997). Mean catches for the previous 10 years show an increase in different locations ranging from 7.7 to 63.0% for pilchards and from 17.8 to 222.1% for anchovies (Neira et al. 1997). This means that the fish stock is still under pressure from continuing exploitation.

Although there is potential for competition between commercial fishery and little penguins along the coast of Victoria, there appears to be no plan to integrate penguin data into the fishery management. The commercial fishery in the coastal waters of Victoria is small and injects approximately 6 million Australian dollars[1] into the state economy (Neira et al. 1997). In contrast, the tourist industry based on little penguins contributes 16 million Australian dollars per year since about half a million people come annually to watch little penguins crossing the beach at Phillip Island (Dann 1992). It seems appropriate to apply the CCAMLR concept that exploitation of resources should not adversely affect natural consumers. This is a unique case where the natural consumer has higher commercial value than the exploited resource.

Seabirds, at the top of the marine trophic level, can be sensitive to changes in the environment and therefore are a useful variable in a fishery management regime using multi-species (Shelton 1992). Seabirds may reduce their reproductive effort if, under unfavorable conditions, breeding could increase their risk of death (Cairns 1987). Fluctuation in breeding performance would be expected in years of food shortage (Krasnov and Barrett 1995). Indeed, the use of seabirds as a monitor of the marine environment is expanding, particularly at places where commercial harvesting may influence the structure of prey populations (e.g. Croxall and Rothery 1991). Low rate or total failure of prey recruitment could cause an earlier response in seabird breeding performance than a later effect in the commercial fishery catch (e.g. Anderson et al. 1980). Monitoring programs of seabird populations have shown correlation between the crash in the fish stocks and variation in seabird breeding performance (Crawford et al. 1983; Wader et al. 1990; Furness and Barrett 1991b; Adams et al. 1992; Furness et al. 1993; Montevecchi 1993).

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[1] Exchange rate of 1 USD$ = 0.62 AD$ in December 1998.

A monitoring program using seabirds to detect any changes requires a long-term study since they are typically k-strategist species; i.e. long-lived with a low reproductive rate and a delayed recruitment into the breeding population. A first step in such a program requires an understanding of the basic biology of the predator species, which includes age-dependent processes and stochastic events (Wooller et al. 1992).

It is crucial to the success of a monitoring program of prey availability to identify variables sufficiently sensitive to detect early signs of changes. Nevertheless, the need for such programs is usually identified when commercial fish stocks and related species are threatened or in a state of decline and when fishing interests seem threatened (Lavigne 1992). Some variables, however, may not detect even the near collapse of the prey stocks (Barrett and Krasnov 1996). Some variables may be masked since monitoring programs rely on correlative analysis rather than on controlled experiments (Williams and Croxall 1990; Barrett 1992; Furness et al. 1993). The power of these correlations comes mainly from observations in poor years in which breeding performance is highly variable (Montevecchi 1993).

Little penguins are found breeding at Phillip Island over 6 to 8 months (Reilly and Cullen 1981). It may be impracticable to incorporate a combined fish-penguin management plan based on such an extended breeding season. There is a need therefore to determine those times in the season when the penguins are most vulnerable to a depletion of food stocks and thus when the fishery should be controlled.

This thesis aims to determine which variables are sensitive to change in prey availability and feasible to monitor fluctuations in breeding performance of individual little penguins at Phillip Island. The little penguin reproductive cycle is studied in detail looking at factors which may affect breeding performance within and between two reproductive seasons. As a species with an extended breeding season, individual little penguins should respond differently on a time scale which may reflect changes in their environment. These variables could be used to develop a program to monitor the impact of the seasonal food fluctuation on the breeding success of little penguins and provide a tool for management of both the little penguin and the fishery.

1.2   Plan of the thesis

The thesis is divided into two parts - practical and theoretical. Chapter one, introduction, sets the scope of this thesis. General methods and calibration of equipment

used throughout this work are in Chapter two. Chapters 3 to 6 deal with the breeding ecology of individual birds. These chapters report on nest attendance patterns, pair bonding, chick growth, foraging trip duration, parental care, meal mass and diet and examine how these variables affect breeding performance during two breeding seasons.

Chapter 7 provides the conclusion of this study. The variables investigated in Chapters 3 to 6 are reviewed to show which variables could be used to establish a monitoring program of prey availability for little penguins at Phillip Island.

2   Method

This chapter describes the different methods and procedures used in this study during sampling. Results are presented for sections which involved calibration of methods or equipment.

2.1   Study site

This study was carried out at Summerland Peninsula during two breeding seasons, 1995/96 and 1996/97, in the south west of Phillip Island, Australia (38°15'S, 145°30'E). The island rises from the Australian continental shelf and lies about 80 km south east of Melbourne, the capital city of the state of Victoria (Figure 2.1). Phillip Island is about 10,100 hectares, 21km by 10km in width, with 96km of coastline. The landscape is of low profile with neither steep hills nor deep river valleys, just a few shallow creeks and some freshwater lagoons and marshes (Edgecombe 1989).
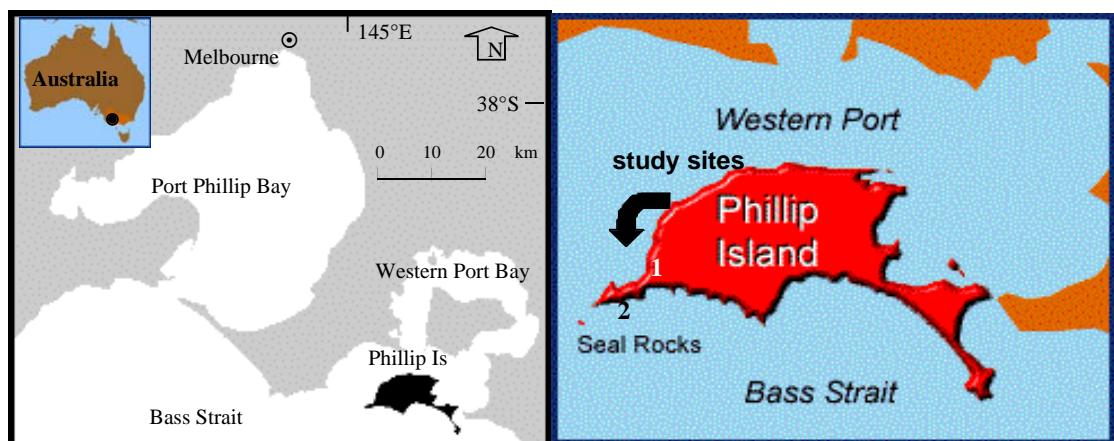
Figure 2.1   Location of the study sites. Map on the left shows Phillip Is in relation to Australia (small map inserted) and the main features cited in this study. The map on the right shows the location of the 2 study sites on the south west of the island. The main research was conducted at site 1, the Penguin Parade colony and the diet study at site 2, Sponge Cove.

The study colony was located within the area known as the Penguin Parade, with approximately 1000 breeding birds (P.Dann, per. com.). The 'Parade' colony is divided into several areas but only birds from area 3 were the subjects of this study (Figure 2.2). The nests included in this study were from an area consisting of the foreshore between the concrete viewing stands and the sand dunes immediately inland from the old board walk area (Figure 2.2).
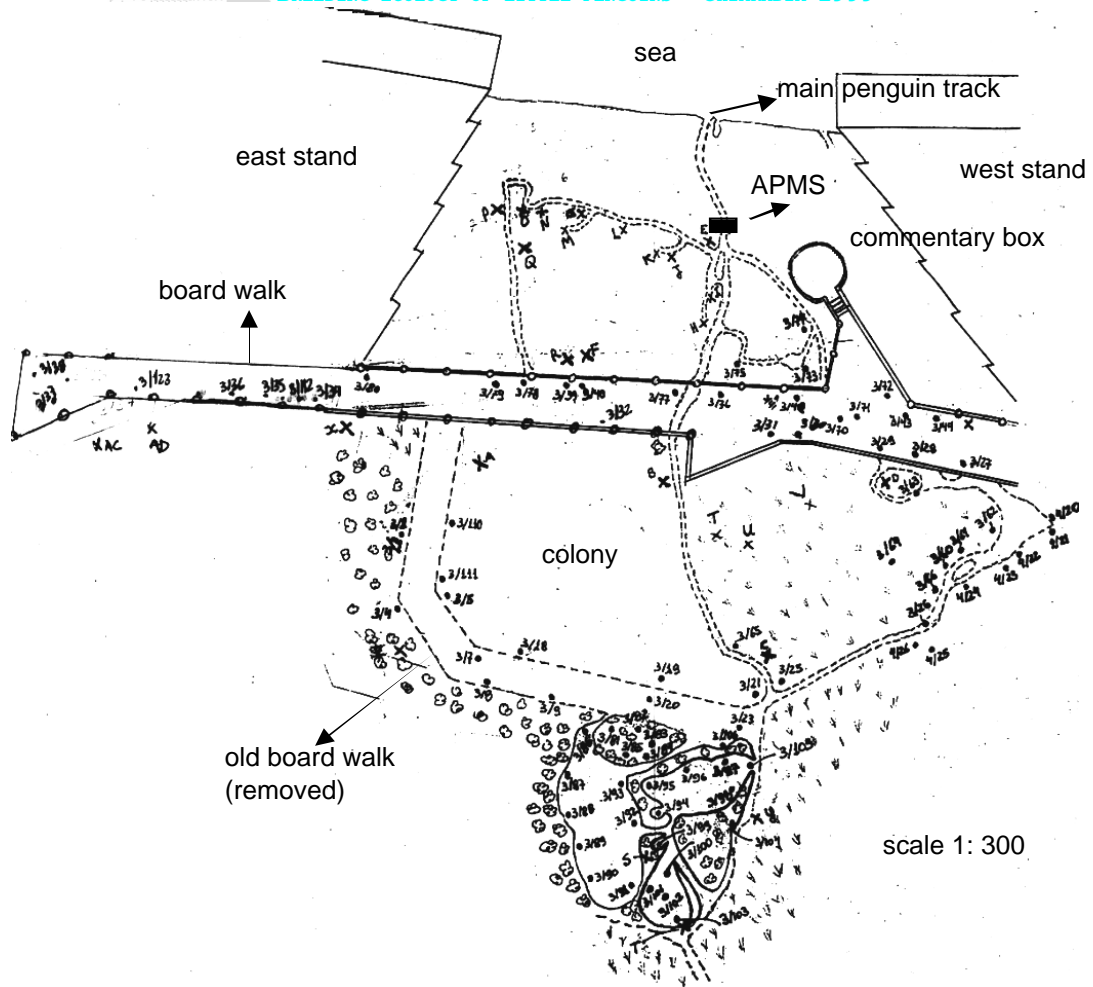
Figure 2.2 Field work map used to locate each marked burrow in the area 3 at the Penguin Parade colony. Burrow is marked with a dot and numbers for artificial burrows and letters for natural burrows.

Little penguins at this site are part of a major tourist attraction where the penguins may be viewed each evening as they arrive and move up the beach. Although they are observed by some 500,000 visitors a year (Dann 1992) there is very little disturbance to the penguins since tourists cannot touch them or move around the colony. People are confined to a board walk or concrete stands out of reach of the penguins.

2.1.1 Oceanography around the study area

The foraging area of little penguins from Phillip Island, in particular during the breeding season, is located in the Bass Strait (Weavers 1992). Bass Strait is a shallow continental shelf channel or sea between Victoria and Tasmania, with an average depth between 50 to 70 metres. It connects the Great Australian Bight to the Tasman Sea and is affected

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by water from both regions. There are two currents that contribute to the Bass Strait circulation: Zeehan and East Australian (EAC) currents (CSIRO 1997).

The following description of the sea surface temperature in Bass Strait was based on an animation video produced by CSIRO[2] Marine Research, Australia for the period of 1990 to 1997 (Cresswell 1997). Sea surface temperature (SST) varies throughout the year with different ranges in winter (10˚C-16˚C), spring (14˚C-18˚C), summer (18˚C-22˚C+) and autumn (14˚C-16˚C). The Zeehan current seems to be more pronounced in winter and EAC appears in summer and recedes northwards at the end of autumn. The Zeehan current weakens between the end of August and the end of September. Sea temperatures rise in spring to 14˚C-16˚C between early October and early December. Sea temperature reached 20˚C or more at the end of December.

The increase in temperature in summer is probably associated with the East Australian current which moves southwards between December and January (Figure 2.3). These warm waters (20˚C+) stayed for a period of 4 to 6 months. About a month after the EAC receded northwards, the SST at Bass Strait dropped below 16˚C reaching 10˚C-12˚C in mid winter.

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[2] Commonwealth Scientific and Industrial Research Organisation
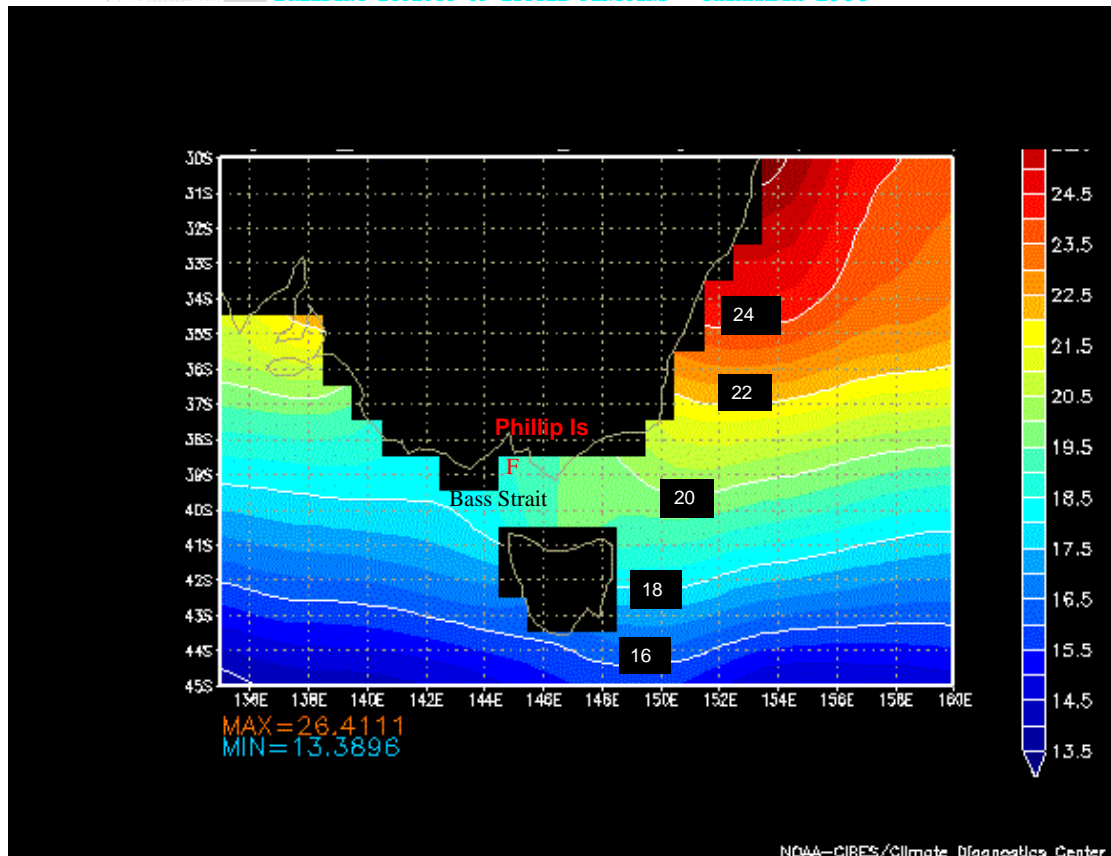
Figure 2.3 **Sea surface temperature in south-east Australia averaged from 9 February to 16 February 1997. The temperature scale on the vertical bar is in Celsius. Top right of the picture shows the Eastern Australian Current and the presence of its warm waters, around 20˚C, in Bass Strait. Image provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, from their Web site at http://www.cdc.noaa.gov/.**

2.2   *Little penguin Eudyptula minor*

Little penguins breed in small colonies and close to food. The onset of breeding varies from year to year but the end of the reproductive season is more predictable (Stahel and Gales 1987, Figure 2.4). Burrows start to be occupied in June and eggs are laid after 2 or 3 months. Laying may occur in May and June but this is unusual (Reilly and Cullen 1981). Birds normally lay 2 eggs and incubate them over 35 days on average. A second clutch is common and a third clutch is occasional (Fortescue 1995). Although a later onset reduces the chance of a second clutch, breeding success is almost identical to a year of early onset (Dann 1992). Chick-rearing takes 7 to 10 weeks (Stahel and Gales 1987). The attendance at the colony increases near the breeding season when birds start to repair their nests for the coming season (Reilly and Cullen 1981). Birds tend to return

to the same area of the colony every year and establish the nest usually within a few metres of the nest in a burrow used in the last season (Reilly and Cullen 1981).

In Australia, little penguins breed in several locations in Tasmania, Victoria, South Australia, Western Australia and New South Wales (Marchant and Higgins 1990). Phillip Island is the breeding ground for 30% of the Victoria population, about 13,000 pairs, which is concentrated on the Summerland peninsula (Dann, pers comm. and Ellis et al. 1998). Phillip Island has an extensive body of biological information based on an uninterrupted study of 25 years (Newman 1992). The bird population has been decreasing, caused by different factors on land and at sea (Dann 1992). Starvation seems to be the principal cause of adult mortality at sea (Harrigan 1992). It seems also that the availability of commercial fish stocks influences the little penguin's breeding success (Hobday 1992). Fortunately, the breeding success is increasing again since measures of conservation have been implemented in order to prevent birds from mortality on land (Peter Dann, pers. comm.).

PHILLIP Is.		TASMANIA	
WINTER	JUN	WINTER	
	JUL		
	AUG		
COURTSHIP	SEP		
INCUBATION	OCT	COURTSHIP	laying
CHICK REARING	NOV	INCUBATION	hatching
	DEC	CHICK REARING	
PRE-MOULT	JAN		fledging
	FEB	PRE-MOULT	
MOULT	MAR	MOULT	
WINTER	APR	WINTER	
	MAY		

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Figure 2.4 Typical life cycle of little penguins at two different locations. The Phillip Island cycle is based on Reilly and Cullen (1981; 1982; 1983) and the Tasmania cycle is reproduced from Gales and Green (1990).

2.3 Daily field work

Visits to the colony were carried out daily for about 500 days throughout two seasons; 1995/96 and 1996/97. Daily observation of 126 nests started on 28 June 1995 throughout a 9 month period in the 1995/96 season and 7 months in the 1996/97 season (Figure 2.2). Additionally, nocturnal visits were made three times a week during pre-breeding of the 1995/96 season. The frequency of visits increased to twice a day during chick-rearing when chicks were weighed in the morning and evening. In the moulting period, the study area was visited once a day and then every second day when no new arrivals were recorded ashore. About 76% of the burrows used were artificial wooden burrows. Small wooden sticks placed at the entrance of each burrow were used to indicate whether birds had entered or left the burrow between visits.

All birds were weighed and sexed and then injected with transponders on the first occasion they were observed in nests at the colony. The bill length was used to determined the sex; males have a larger bill than females with length greater than 13.4 cm (P. Dann, pers comm.) Unbanded birds were fitted with stainless steel flipper bands. About 76% of these birds were already banded as either chicks or as adults when they were first recaptured at the breeding colony. Because nests have been checked for unbanded birds at regular intervals since 1978 and birds return to the colony at age of 2 or 3 years (Dann and Cullen 1990) it was assumed that all adult birds were 2 years old at banding.

The presence of birds with transponders was recorded daily in the colony by a portable transponder reader, a box logger with a long rigid tube which can interrogate transponders through both natural and artificial burrow walls.

Those pairs which raised at least one chick to fledging stage were considered successful. A failed nest was one in which an egg was laid but no chick was fledged.

2.3.1 Implanting of transponders

A total of 315 birds had transponders implanted: 227 were adults and 88 chicks prior to fledging. Transponder tags which may be implanted under the birds' skin, were used to identified individual birds. Transponders (transmitter + responder) are passive

identification devices which receive electromagnetic waves from a transponder reader and then rebound data, i.e. send the transponder number back to the reader display. Transponders are available on the market in different sizes, makers, transponder injectors and, most important, reading range. TIRIS™ transponder, a glass coated tag 23mm long and 3mm in diameter was selected since it provided a wider reading range (about 500 mm) than other transponders giving more reliability to the automated system.

A dead penguin was injected with a transponder several times to master the injection technique. Further, a female little penguin was tagged and kept under observation at the Penguin Reserve Rehabilitation Centre for two days. The injection area bled a little after the injection but stopped soon after. The wound could not be found the following day and no sign of sensitivity, infection or any change in behaviour was observed. In the field, penguins with transponders had no signs of inflammation. Betadine® antiseptic was applied during the injection to avoid infection in the implanted area (Clarke and Kerry in press).

The transponder was injected subcutaneously between the penguin's scapulas. This injection site was preferred over the nape of the neck which is commonly used in such studies (Kerry et al. 1993; Clarke and Kerry in press) since there is less loose space between the skin and the muscles at this site. Transponders are unlikely to migrate from this injection site.

Three transponders were lost from the injection site and two transponders malfunctioned. The application of surgical glue (Vetbond, 3M) to seal the injection site negated transponder loss.

2.4   Automatic Penguin Monitoring System (APMS)

The manual method currently used to study little penguin attendance at the colony requires the removal of birds from their burrows to read the flipper band number. Although it is difficult to assess the disturbance caused by this method, it may disrupt the colony if visits are repeated at short intervals. To overcome this problem an automated penguin monitoring system (APMS), developed by the Australian Antarctic Division, combined with transponders was used to record individual birds as they entered or left the colony (Kerry et al. 1993). Birds arriving on the beach moved in groups into the breeding area in the sand dunes. The majority of birds in the study

colony followed the same track and were logged by the APMS which was placed on their pathway on 6 October 1994 between the concrete stands near the commentary tower (Figure 2.5).
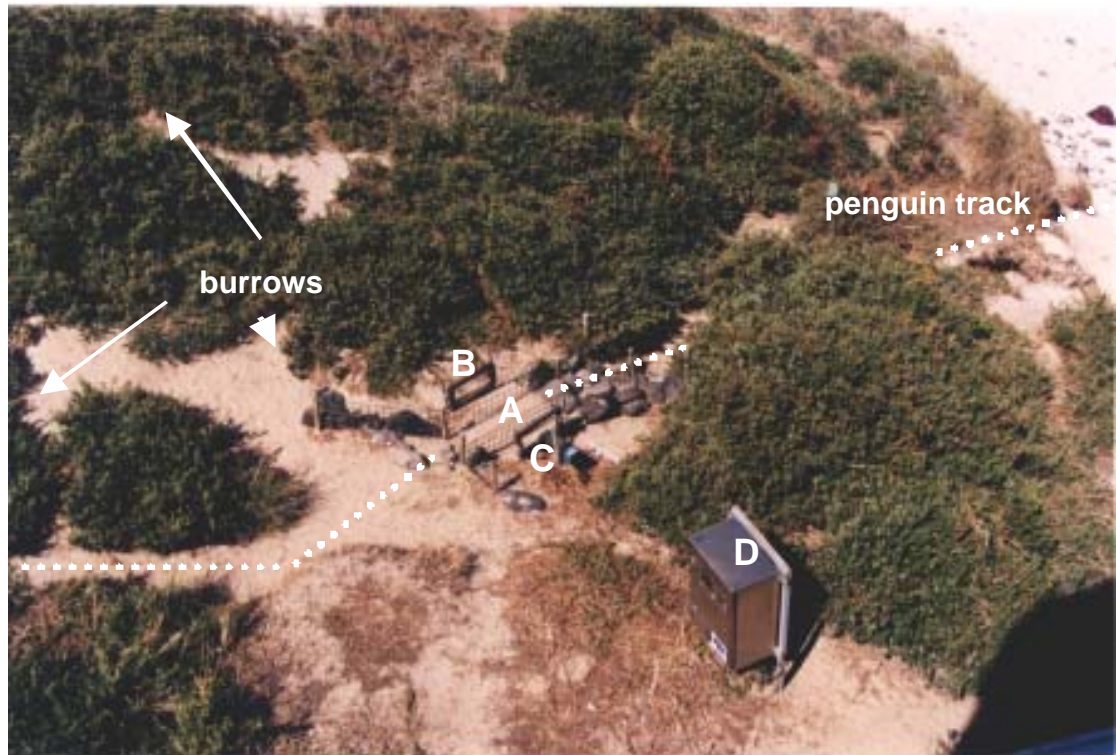
Figure 2.5   **The APMS was placed on pathway of the penguins. As penguins walk to and from their burrows in the colony, they cross the platform (A). Each bird with transponder was identified by the transponder reader (B) and its direction detected by breaking the beams (C). Each record was then stored in a microprocessor system (D).**

The APMS automatically recorded the transponder number, date and time and direction of each bird. The system consists of four main parts: a weighbridge, an electronic transponder reader, a system controller and a data logging apparatus. The weighbridge, a flat low-profile stainless-steel platform, was placed in the pathway of the penguins which were weighed when crossing the bridge. The transponder reader identified individual birds with injected transponders. Infra-red beams placed on the platform informed the nature of crossing, eg if the birds were coming ashore or leaving the colony. The weight, transponder number, nature of crossing and date/time, were recorded by a microprocessor system with enough memory to store the crossing data on 16,000 penguins. Two or more birds were recorded as crossing error. Single crossing may have also presented error when a flipper breaks the infra-red beams before the

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body or when a bird stopped and turned around before completing the crossing. The APMS was cabled to the commentary tower where penguin crossings could be monitored using a portable computer (Figure 2.2). A modem linked to the APMS allowed remote connection with the system i.e. the data could be accessed over the telephone during the off field-work season.

Birds which followed an alternate track were logged by a simpler system which recorded transponder number only. Night visits, i.e. when birds arrived and departed during the same night, could not be recorded if they did not cross the APMS in any direction.

A portable transponder reader was used to check daily bird presence in individual nests. This reader was able to detect transponders through both artificial and natural burrow walls without disturbing the birds and reduced by 75% the time required for nest checking compared with manual methods.

2.4.1 Limitations of the APMS

The infra-red beams require that birds should break the beams in sequence to flag a correct direction. Birds were breaking the beams several times before crossing the platform which enabled the system to record the correct direction of the birds. A tunnel placed on the weighbridge was probably the reason for the birds' behaviour. Birds had to crouch down to cross through the tunnel breaking the beams several times by moving the flippers and head up and down. However, the direction of crossing had less priority than the tunnel. The tunnel prevented birds from crossing the platform in groups. The penguin direction could be worked out since little penguins normally come to and leave the colony in a specific period of time (Klomp and Wooller 1991). Birds arriving or leaving outside regular times had their direction figured out by the double crossing in the same night (in and out) or by the presence/absence in the colony during the daytime survey following the night that crossing occurred.

The weighbridge was designed to provide weights with a margin of error of 20g. On the 1995/96 field season, however, the system was registering variations of plus/minus 100g. The source of the problem was identified as the low sensitivity of the weighing platform, which was originally designed for measuring weights much heavier than little penguins. The weighbridge was working at the lower end of its scale which amplified the error and consequently lessened the accuracy and precision of output weights. A

new and reliable weighing platform were replaced in the middle of the 1996/97 field season. However, the data generated were related to a short period of time and did not allow inter- and intra-seasonal comparison and therefore weights from the APMS were not included in this study.

The APMS system was highly reliable for recording bird crossings and proved to be a crucial tool in examining foraging trip duration and attendance patterns over a continuous period of time.

2.5 Bird behaviour on the weighbridge

The APMS requires a single penguin to cross the platform at a time. Two or more birds on the platform cause error on the output weight although the individual bird is still identified. A calibration was conducted to induce single crossings on the platform. Birds were counted during the second half of the 1994/95 breeding season. In the period between 13 January and 28 March 1995, crossings were recorded on 27 evenings and 21 mornings. The crossings were categorised as:

- single bird

- single birds with one chick standing on the platform

- two birds

- three birds

- more than three birds

Little penguins come ashore and leave at a very defined time. The majority arrive one to two hours after dusk and depart one hour before dawn (Klomp and Wooller 1991). They always move in groups when walking towards their burrows which made it difficult to have one bird at a time crossing the platform. In addition, birds tend to preen (rearrange and wax the feathers) and rest on flat surfaces when moving along their track and the weighbridge platform turned out to be a perfect place for such behaviour.

When birds crossed in a line with no interval between them, the final number recorded represented the total birds that crossed the weighbridge after the last one stepped off. Most of these cases fell into the "three or more birds" category. Evening and morning counting were analysed separately since birds tended to behave differently at these times.

2.5.1 Evening behaviour

Flat areas along the pathway are very popular for preening and resting. When birds reach a flat area after climbing a hilly stretch they stop for a while before continuing the journey. This natural behaviour was responsible for the presence of two or more birds on the weighbridge. Figure 2.6 sumarizes all evening crossings. In the first counting day, 13 January, only 17% of birds were recorded doing a single crossing. Double and triple crossings occurred most frequently.

When penguins climb a barrier they first measure the height stretching the bill over the object to reach the top. If the bill touches the top they can jump up and overcome the obstacle (Reilly 1994). Little penguins also tend to make a short run after jumping down from a barrier. Based on this behaviour, modifications were made on the pathway around the weighbridge to induce single crossings. Penguin-width fences were set up along the weighbridge. Rocks were placed on both sides (in and out) to slow down birds and to allow only a single bird to reach the platform each time. After these modifications, on 19 January, about 61% of birds were making single crossings and the other 39% of birds were crossing with two or more birds (Figure 2.6).
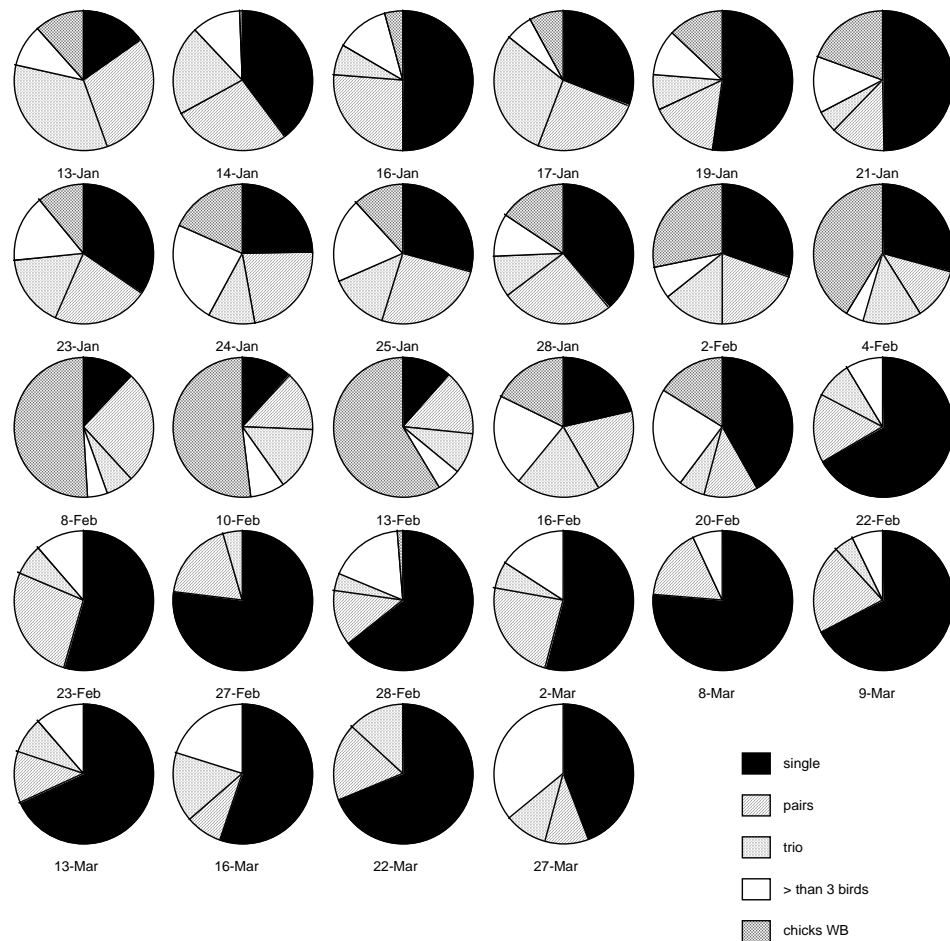
Figure 2.6 **Bird crossings on the APMS platform as they came ashore in the evening. Sequence of 27 sampling days showing the proportion of different type of birds' crossing on the APMS platform. Graphs are in chronological order from left to right. Sampling date is represented at the bottom of each graph.**

This was a satisfactory result but some chicks aging four weeks or older introduced another source of error on the APMS platform. About one hour before parents arrive from the sea, chicks leave their burrows to wait for their food. Apparently they do not recognise the parents so they beg food from every single adult which comes across their way (Reilly 1994) . Chicks found quickly that the weighbridge was the perfect place to intercept the adults on the way up to the colony. The number of single crossings with a chick on the APMS platform increased sharply as shown on 10 February 1995 when 52% of crossings were with single adults but with a chick on the weighbridge (Figure 2.6). Most of the double or more crossings of adults occurred also with a chick on the weighbridge. Single crossings happened only when chicks stepped off the weighbridge chasing adults along the track. A sand platform was placed just below the weighbridge

to create an alternative place for the chicks to harass the adults. Subsequently, the figure turned to 16.3% single crossings with a chick and 41.8% successful single crossings on 20 February (Figure 2.6).

A further modification was made by placing a mesh-made tunnel over the weighbridge to prevent chicks from standing on the weighbridge. This tunnel made the platform an uncomfortable place for the chicks to stand and induced the adults to cross one by one. Birds had to crouch down to cross the tunnel which made a double crossing more difficult as shown on 22 February (Figure 2.6). After this change, the range of single crossing varied from 55.4% to 76.9% averaging 65.3% (n = 11 sessions).

2.5.2 Morning behaviour

The modifications introduced on the weighbridge did not reflect in the morning crossings as successfully as it did in the evening crossings. Birds tended to behave differently when they were leaving the colony in the morning before dawn. They went to sea in small but clustered groups of 3 to 10 birds. Attempts to split these small groups were only partly successful. Modifications on the pathway using rocks and corrugated sheets had slowed the birds but did not improve the rate of single crossings as observed between 16 January and 21 February (Figure 2.7). The number of single crossings improved after the tunnel was placed on the APMS platform on 23 February with 46.8% of single crossings (Figure 2.7). Single crossings averaged 21.9% before and 32.6% after the tunnel placement.
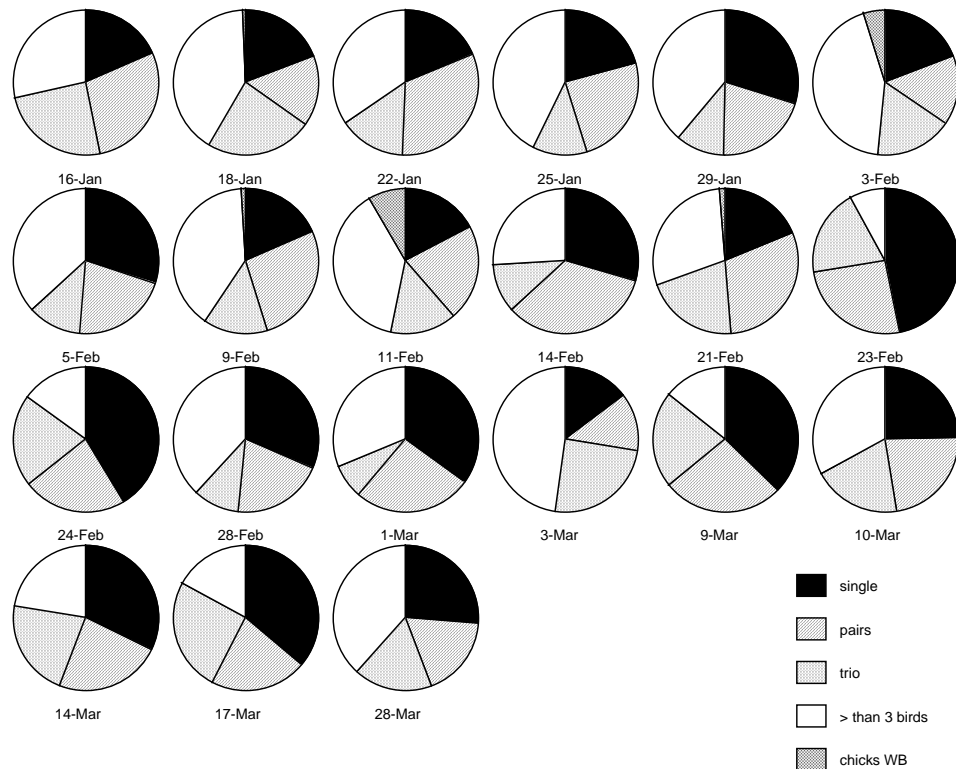
Figure 2.7   Bird crossings as they leave the colony in the morning before dawn. Sequence of 21 sampling days showing the proportion of different type of birds' crossing on the APMS platform. Graphs are in chronological order from left to right. Sampling date is represented on the bottom of each graph.

2.6   Taxonomy and terminology

Scientific names of fish used in this study were based on the Codes for Australian Aquatic Biota managed by the CSIRO Division of Marine Research and available in their Web site at http://www.marine.csiro.au/caab/commercial.html.

The common names of birds and prey items are not given capitals except where they contain proper names (AGPS 1992).

2.7   Statistics

All statistical analyses were performed using the Systat package (Wilkinson 1989). Graphs were produced in Deltagraph and Sysgraph. Bars represented in the graphs are standard errors. In the text, averages are given as mean ± standard deviation unless stated otherwise.

All data treated on parametric analysis were tested for normality, homogeneity, skewness and kurtosis (Wilkinson 1989). Clumped or dispersed distributions were transformed to normal distribution by use of appropriate transformations.

Anova is not robust to outliers so they were identified using Studentized residuals and removed from the analysis of variance (Wilkinson 1989). After using ANOVA, Tukey-Kramer adjustment was used for multiple comparison which adjusts unequal n's by a harmonic mean n (Wilkinson 1989). Results are presented as F values with degrees of freedom and sample size ($F_{DF, n}$). The exact value of P is shown unless it is smaller than three digits and then $p < 0.001$ is used.

Chi-square is represented as X^2_{DF}.

In independent t tests where the number of cases differed between groups, both the separate and pooled variances were calculated. Separate variances use the separate variances within groups while pooled variances use the pooled within-groups variance (Wilkinson 1989). When the results differed substantially, I used the separate variance which is more conservative than the pooled variance. In this case, degree of freedom differed substantially from the sample size and sometimes the degree of freedom was expressed in decimals.

3 Nest attendance and breeding success in the little penguins *Eudyptula minor* at Phillip Island, Australia[3]

3.1 Introduction

Little penguins, *Eudyptula minor,* have a long egg laying period and visit their breeding grounds throughout the year. Occasional visits occur during the pre-breeding season but intensify some weeks before the onset of the breeding period (Kinsky 1960; Reilly and Cullen 1981; Stahel and Gales 1987).

The onset of egg laying of the little penguin at Phillip Island varies from year to year between late August and mid November (Dann 1992). The cause for the variability of the date of onset of breeding is unknown although Mickelson et al. (1992) suggested that it may relate to the effects of changes of sea temperature in July and August. The spread of egg laying dates within a season also varies between three weeks and three months (Reilly and Cullen 1981).

Given this variability it might be expected that the pattern of attendance of breeding birds at their nest would vary between years and within the season. Although there are some estimates of the overall period of time a bird spends ashore (eg Hodgson 1975; Reilly and Balmford 1975; Reilly and Cullen 1981; Stahel and Gales 1987), very little information is available for the little penguin on the attendance of individual birds in the colony throughout the breeding cycle and differences in attendance patterns for successful and failed breeders (sensu Williams 1995). This absence of data is due in part to the need to remove birds from their burrows to read bands (Kinsky 1960; Hodgson 1975; Reilly and Cullen 1981), which may cause undesirable disturbance to the individuals and therefore imposes limitations on the frequency with which birds in a colony can be visited (Dann, per. comm.). The use of new technology has overcome this problem and as described in Chapter 2 birds can be identified in their burrows without handling them.

This chapter describes observations made at Phillip Island on the daily attendance pattern of individual little penguins during two breeding seasons, 1995/96 and 1996/97. The patterns of successful and failed breeders during the pre-breeding, incubation and

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[3]Chiaradia, A. F. and K. R. Kerry (1999). "Nest attendance and breeding success in the little penguins *Eudyptula minor* at Phillip Island, Australia." Marine Ornithology 27: 13-20..

chick-guard periods during the 1995/96 season are compared. Details are given for shifts and foraging trip duration during incubation and chick-guarding.

3.2 Method

The field procedures and statistics used in this study are described in Chapter 2 – Method.

Most birds arrive at dusk and depart at dawn on the same night or one or more mornings later. No visits or departures occurred during daylight hours, although a few birds arrived and/or departed at irregular hours during the night. A bird which arrives one night and departs the following dawn thus will have spent about 8 hours ashore and a bird which remains during daylight hours will have spent approximately 32 hours ashore (depending on day length). Thus birds which change over in their incubation or guard shift each night will each spend alternately about 32 hours ashore. During the compilation of attendance statistics for this study the first 8 hour period ashore is ignored and time is measured in days meaning a full daylight period is spent ashore.

The breeding season was considered to start at courtship when pairs were seen together for the last period of time before the pre-laying exodus. Courtship started approximately one month (maximum 31 days) before egg laying.

The incubation period was measured from the date of egg laying to the date of hatching of the first egg. Nests were checked daily for eggs until the first egg was laid. No regular attempt was made to determine time of laying of the second egg to avoid undue interference but several observations showed that second egg was laid one day apart from the first egg. It was assumed that for each nest, incubation started when both eggs were laid, i.e. one day after the first egg was laid . The guard period was taken to end at the last date a parent remained with the chick during the daytime.

During the incubation and the chick guard periods parent birds alternated attendance at the nest. While one bird attended the eggs or chick the other foraged at sea. Thus incubation shift and foraging trip duration are complementary events. Where the focus is on the activity at the nest during incubation the event is referred to as the "incubation shift". Similarly when the focus is on foraging the event is referred to as "foraging trip duration".

The analysis of difference between successful and failed breeders was concentrated in the first season but general pattern of attendance is related to both season. In the season

1995/96, eggs were laid in 53 nests and two nests had a second clutch and therefore, in this season the sample size was n = 55 nests. In the season 1996/97, the sample size was n = 54 nests. Thus, the sample size used in the analysis was n = 109 nests unless otherwise stated in the text. In the season 1995/96, nest 22 had two males involved with one female but those males were never recorded together in the same burrow (Figure 3.1).

Mean length of incubation shift (I) of both parents as related to the day of hatching (d_0) was calculated for the 1995/96 season. The shift length was recorded on the last day before the relieving mate returned to the nest.

$$I = \frac{\sum\limits_{n=1}^{48}(Ln)}{Sd}$$

$Ln=$ the length of each incubation shift completed on day d

$S_d=$ the number of incubation shifts completed on day d

$S_{dmax}=$ 48 i.e. the maximum number of shifting nests in a day

$d=$ the day on which the change over of partners was observed, i.e. had occurred on the previous night.

$d_0 =$ the day of hatching and d ranges from d_0 to d_{-36}.

Logistic regression analysis (McCullagh and Nelder 1983) was used to compare several variables against successful or failed breeders.

3.3 Results

3.3.1 Phases of attendance

The bird attendance had a similar pattern in both seasons and the description of different phases is based on the 1995/96 season.

Figure 3.1 shows the attendance patterns from 28 June 1995 to the end of the guard phase in the 1995/96 season in chronological order of egg laying. Attendance patterns of the adults after the guard period are not shown but post guard was also investigated and it is discussed in Chapter 5. Most of the deaths occurred after the chick guard period. The first egg was laid on 4 October 1995 and egg laying was essentially completed by 31 October 1995 when 49 nests had eggs, 3 females laid in November and one in December (Figure 3.1). Two nests which failed had a second clutch which also failed (Figure 3.1, nests 22 and 47). All chicks had fledged by 2 February 1996.

It can be seen by focusing on the patterns of attendance at the nest (Figure 3.1) that six phases are discernible. Four occur leading up to egg laying, namely inter-breeding, courtship, the pre-laying exodus and pre-laying which are followed by incubation and the chick guard period. These phases are summarised diagrammatically in Figure 3.2.

3.3.2 Attendance before egg laying

Birds of both sexes made occasional visits to the colony during the interval between breeding seasons. Rarely were both members of the future breeding pair present at the same time.

The courtship period began approximately one month (maximum 31 days) before egg laying and lasted on average 5 days for females and 5.5 days for males (range 1-9 days). Males arrived earlier than females in 60% of the cases. Males and females arrived at the same time in 25% of cases and only 15% of females arrived earlier than males in the colony. After courtship the females departed, i.e. a pre-laying exodus which lasted 10.5 days. The males also returned to the sea but for a significantly shorter period of 8.7 days (Table 3.1) tending to leave later and return earlier than their partner.

Following the pre-laying exodus 66% of males returned on the same day or 1 – 2 days ahead of the females. In the 1995/96 season, one pair was recorded only on the day of egg laying (nest 34, Figure 3.1) and two males were recorded only after egg laying date (nests 35 and 41, Figure 3.1). They may have stayed in another burrow outside the study area during the courtship and pre-egg periods or made only night visits to the colony and were not ashore during the day.

The females remained ashore 5.6 ± 3.1 days during which time a clutch of two eggs was laid. The first egg was laid 4.9 ± 2.8 days after arrival. The male stayed in attendance 4.4 ± 3.5 days and was usually absent on the morning after the first egg was recorded. There was no significant difference between ages of males and females at breeding (Table 3.1).

variable	female			male			t test	
	mean	SD	n =	mean	SD	n =	t value	p =
Total period ashore before laying (days) *	11.2	5.4	53	14.8	8.0	55	2.74	0.007
Number of visits before laying *	3.1	1.5	52	4.5	2.6	55	3.38	0.001
Pre laying exodus (days)	10.5	4.8	100	8.7	3.8	103	3.01	0.003
Laying period (days)	5.1	2.6	106	3.8	3.4	108	3.24	0.001
Incubation shifts (days)	3.0	1.8	103	3.1	1.2	104	0.26	0.797
Number of foraging trips during incubation	6.8	2.7	103	6.7	2.6	104	0.26	0.797
Chick guard shifts (days)	1.2	0.5	96	1.1	0.2	96	1.68	0.095
Number of foraging trips during chick guard	7.0	2.8	100	6.9	2.6	99	0.43	0.671
Breeding age (years)	6.8	3.2	78	7.3	3.5	72	0.92**	0.360

Table 3.1. **Comparison of attendance between male and female little penguins at Phillip Island using several variables. The data correspond to two breeding seasons, 1995/96 and 1996/97, except for the two first rows indicated by (*) relating to the 1995/96 season. Variables were measured on days, counting numbers or years as indicated in each row. Statistically significant values are highlighted. Data on age of breeding birds were transformed for the t test (**). n = number of individual birds. All variables measured in a period of days refer to time ashore except to pre-laying exodus which is the absence in the burrow.**

3.3.3 Incubation shifts

Incubation lasted for 35.9 ± 2.5 days (range 31 - 50 days, n = 109 nests) which was similar to previous estimates for Phillip Island and Tasmania (Hodgson 1975; Reilly and Cullen 1981). The incubation period had the same length in both seasons irrespective of whether the birds later failed or bred successfully. The wide range in incubation period is attributed to interrupted incubations. In the 1995/96 season, eleven nests had eggs unattended from one to 6 or more days. Four of these nests had eggs which hatched although they were left unattended from one to six days which were not consecutive. Eggs which were unattended for more than three days showed an increased incubation period and those unattended for periods longer than six days did not hatch (n = 7 nests, Figure 3.1). Unattended eggs were not recorded in the season 1996/97 but two nests had infertile eggs which were incubated for 48 and 50 days, respectively.

Figure 3.3 shows the average length of each incubation shift as related to the point of hatching in the season 1995/96. The shift length was recorded on the last day before the relieving mate returned to the nest. The shift duration was 2 to 3 days for the first half of the incubation. About 17 days before hatching the shift duration increased to 4 to 5 days or more before decreasing again to a shift duration of 1 to 2 days, three days before hatching. It was noted that on 1 –2 November 1995 there appeared to be a change from short to long incubation shifts irrespective of the egg laying date (Figure 3.1).
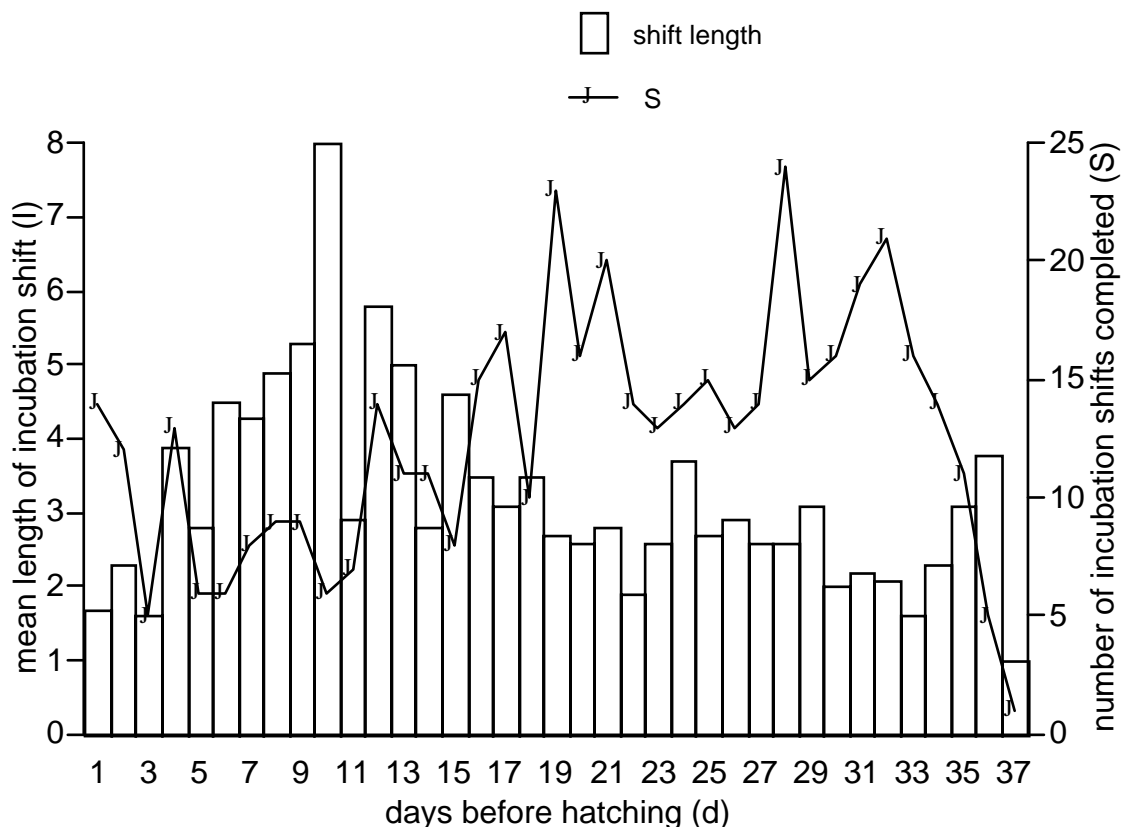
Figure 3.3 **Mean length of incubation shift (I) as related to the day of hatching (d_0) for the 1995/96 season. The shift length was recorded on the last day before the relieving mate returned to the nest. Data are reported for both members of the pair. S is the number of incubation shifts completed on a particular day. See method in this chapter for detail on the calculation of the mean length of incubation.**

Individual birds completed on average 6.8 incubation shifts which lasted on average 3.1 days. There was no significant difference between males and females in the length of their incubation shifts (Table 3.1). However successful breeders (males and females) had shorter shifts during incubation than failed breeders (Table 3.2). It was

found that the number of foraging trips and length of incubation shifts were significantly different between successful and failed breeders (Table 3.2 and 3.3).

variable	success			failure			t test	
	mean	SD	n=	mean	SD	n=	t value	p value
Number of visits before laying *	4.0	1.4	38	3.9	2.6	56	0.87	0.385
Laying period (days)	4.5	3.0	117	4.3	3.2	97	0.39	0.698
Incubation period (days)	35.7	1.2	59	36.2	3.6	43	1.49	0.159
Incubation shifts	2.6	0.9	118	3.6	1.9	89	4.62	< 0.001
Number of foraging trips during incubation	7.8	2.6	118	4.3	1.9	89	7.63	< 0.001
Length of chick guard (days)	19.1	5.6	59	13.8	4.8	40	7.20	< 0.001
Chick guard shifts	1.1	0.2	118	1.2	0.6	74	1.35	0.182
Number of foraging trips during chick guard	8.1	2.3	118	5.3	2.4	81	8.27	< 0.001
Breeding age (years)	7.6	3.0	81	6.4	3.6	69	3.22	0.002

Table 3.2   Comparison of attendance between successful and failed breeders using several variables . The data correspond to two breeding seasons, 1995/96 and 1996/97, except for the first row indicated by (*). Variables were measured in days, counting numbers or years as indicated in each row. Significant values of t test are highlighted. Data on age of breeding birds were transformed for the t test. The (n =) is the number of individual breeders except for incubation period and length of chick guard which are the number of breeding pairs.

3.3.4 Chick guard period

Parents guarded the chicks for 17 ± 5.9 days (n = 109 nests). Females and males spent similar amount of time ashore with the chicks and they made the same number of foraging trips (Table 3.1). Successful breeders guarded their chicks longer since they made more trips but their length of shift was similar to failed breeders (Table 3.2).

variable	female	male
Number of foraging trips during incubation	***	***
Incubation shifts	**	**
Attendance before laying	*	n.s.
Number of foraging trips during chick guard	n.s.	n.s.
Number of visits before laying	n.s.	n.s.
Chick-guard shifts	n.s.	n.s.

Table 3.3   Within sex comparisons between successful and failed breeding birds using a logistic regression analysis (McCullagh and Nelder 1983). Asterisks denote significance to the 0.05 (*), 0.01(**) and 0.001(***) levels.

3.3.5 Timetable, age and breeding success

The mean egg laying date of successful breeders was approximately two weeks earlier than those that failed which was consistent in both 1995/96 ($t_{108}= 4.07$, p < 0.001) and 1996/97 ($t_{105}= 7.79$ p < 0.001) seasons. In the season 1995/96, one third of the study

population bred successfully, ie they managed to fledge at least one chick. Almost all successful breeders laid their eggs in the first two weeks, prior to 15 October, whereas more than 50% of failed breeders laid eggs after this date (Figure 3.1). In contrast, two thirds of the study population bred successfully in the season 1996/97. Failed breeders started to lay eggs only three weeks after egg laying started when about 85% of successful breeders had already laid their eggs.

Figure 3.4 shows the distribution of breeding birds by age class. About 67% of the breeding birds were between three and eight years old. Successful breeders were on average one year older than failed breeders (see last row on Table 3.2). These age classes agree with the age distribution of successful breeding birds per lifetime reported by Dann and Cullen (1990).
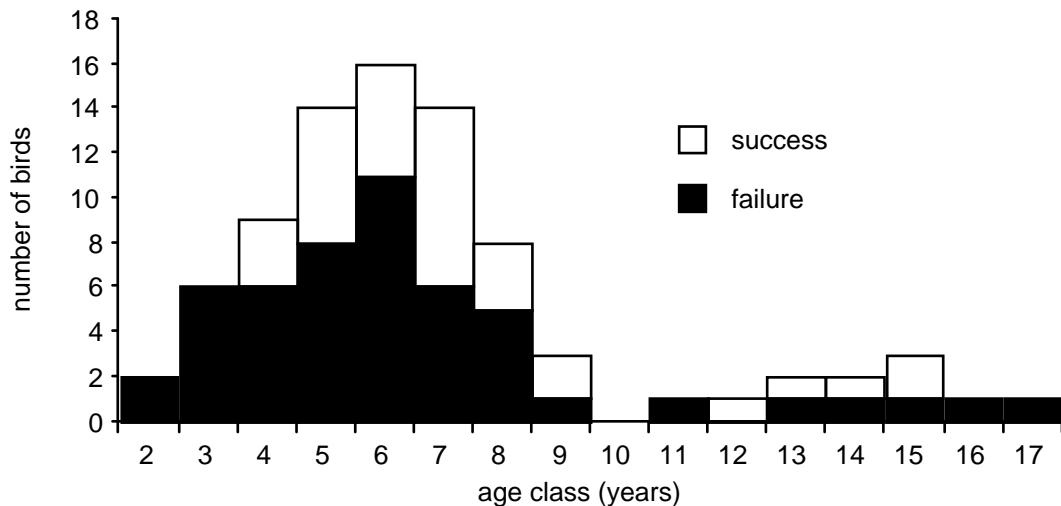
Figure 3.4   The distribution of frequency of age classes of successful and failed breeding little penguins in both seasons, 1995/96 and 1996/97.

3.4   Discussion

This chapter presents a detailed investigation of the attendance pattern of male and female little penguins from the time of first arrival at the beginning of the breeding season to the end of the chick guard period. Courtship was separated from the egg laying period by a pre-laying exodus for males and females and the period of absence of females during this exodus is on average 10 days in both seasons. This finding adds another phase in the typical pattern of the little penguin life cycle not reported previously (Richdale 1940; Kinsky 1960; Reilly and Cullen 1981; Stahel and Gales 1987; Gales and Green 1990).

The incubation period from egg laying to the chick being fully separated from the shell was 36 days. The period was lengthened in the few instances where incubation was interrupted intermittently. The incubation period was similar to the 33 to 37 days range (n = 7) reported for Phillip Island by Reilly and Balmford (1975) who measured incubation from the laying of the second egg to hatching of the first egg. There were no changes in the incubation length between successful and failed breeders and between seasons which suggests that the length of incubation does not respond to seasonal or individual fluctuations.

3.4.1 Incubation shifts

The duration of incubation shifts varied but on average took 3.1 days which is within the range of one to eight days recorded at Bruny Island and Phillip Island (Marchant and Higgins 1990). These observations differ markedly however from data reported by Kinsky (1960), who from limited periods of observation, reported that shifts lasted only hours with females conducting more of the incubation. This study agrees with Williams (1995) who commented that Kinsky's results may be unusual.

The little penguin, in keeping with other species of penguin and seabirds, must coordinate the foraging trips between partners so that one parent is available to feed the chick at hatching. This means that no matter how the incubation foraging trips vary over the 36 day incubation period the birds must reduce the duration of their trip as hatching approaches. The present results suggest that both internal (hormonal) and external (environmental) factors are involved in the determination of length of incubation shift in little penguins. These factors influence the foraging bird rather than the incubating partner since this bird has the freedom to determine when the foraging period, and hence the incubation shift of its partner, must end.

The pattern of incubation shift duration shown in Figure 3.3 presumably has a physiological basis as the changes shown relate to the point of hatching even though the actual date of hatching was spread over a 6 weeks period. Davis et al. (1995) showed for the Adélie penguins that high concentrations of progesterone occur in males and females just before hatching and suggests that even if it is not progesterone that precipitates the return of the penguins it may be at least associated with whatever triggers their return. A hormonal mechanism similar to this may operate in the little penguins. It is possible that the increase in foraging trip duration in the second half of

incubation occurs at a time when blood progesterone levels are low and that the decrease in foraging trip duration at the end of incubation is brought about by an increase in this hormone.

The observation that the length of incubation shifts tended to increase from 1 – 2 November 1995 for most pairs irrespective of date of egg laying suggests that this change was related to environmental conditions. Possible explanations include the active movement of prey away from the immediate foraging zone or changes in the environment. All birds reverted to daily foraging trips at hatching. This event may not happen every year as many factors could affect prey distribution and breeding chronology (Dann 1992; Mickelson et al. 1992). Chapter 5 discusses possible causes of the intra- and inter-seasonal fluctuations in foraging trip duration.

3.4.2 Guard period

A day trip for little penguins means a foraging area of about 8 - 15 km radius from the burrow (Weavers 1992; Collins et al. 1994). Using birds with radio transmitters, Collins et al. (1994) found that chick fledging ie breeding success was associated with frequency of trips. Birds which performed short trips were more successful than those making longer trips. Short trips could then indicate that food was available close to the colony during chick rearing. Regardless of their breeding performance and inter season fluctuations, however, all breeders made day trips at guard period. This suggests that the foraging trip duration in the guard period does not correlate with fluctuation of food supply.

The availability of food, its proximity to the colony and the prevailing weather conditions presumably will all influence the period the chick is guarded. Chicks were brooded for a total period averaging 17 days in the present study. This period is in agreement with the three weeks suggested by Stahel and Gales (1987) and the period of 10 - 21 days concluded by Kinsky (1960). Williams (1995) noted without reference that this period lasts 20 - 30 days. Moreover, successful breeders guarded their chicks for 5 days longer than failed breeders. A chick must be raised to sufficient size to gain independence and be able to regulate its own body temperature (Baudinette et al. 1986; Stahel and Gales 1987; Williams 1995). The extra 5 days being brooded by its parents may be crucial for the satisfactory growth of the chick. A possible inter-seasonal fluctuation of the length of the chick rearing period between a poor and a good year of

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food supply as observed in other seabirds (Williams and Croxall 1991; Murphy 1995) is discussed in Chapter 5.

3.4.3 Female versus male attendance

Before egg laying, including the interval between breeding seasons, males spent 24% (about four days) more time ashore than females. Males arrived early at the colony for the courtship; about four weeks before egg laying date. Both male and female went to sea after courtship for the pre-laying exodus and then the male returned first again for the egg laying period. After the egg laying period there was no difference in the attendance pattern between sexes. These differences in attendance patterns occur during the pre-egg periods because males and females are engaged in different activities. Males need to be in the colony as often as possible to defend territory and possibly to reduce the risk of losing paternity (see Chapter 4). On the other hand, females should be at sea to accumulate energy to cope with the egg laying period. After egg laying, both sexes are involved in the same activity and share common tasks; therefore they have a similar attendance pattern.

3.4.4 Breeding timetable, age and breeding success

Reilly and Cullen (1981) noted that for different seasons the later the onset of breeding the poorer breeding success was likely to be. This study observed further for these two seasons at least, which commenced later than usual (Reilly and Cullen 1981), that on average the earlier breeders in the season are more successful. Successful pairs had shorter incubation shifts and undertook more foraging trips than failed breeders during incubation and chick guard period respectively. This suggests that these birds were able to forage more efficiently than their later breeding counterparts. It is interesting to note that the duration of foraging trips increased from about 1 November 1995. This suggests that food became generally unavailable at that time even to birds which earlier apparently had no difficulty in foraging.

The observation that attendance patterns varied between successful and failed breeders, that earlier breeding birds were more successful and that the attendance pattern for the whole colony could change at much the same time suggest that the little penguin is responding to changes in the availability of food within the foraging zone. The reason why some birds were able to breed more efficiently than others may be related to their age. This study found that successful breeders were on average one year older and thus

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more experienced than failed breeders. Moreover successful breeders laid eggs about two weeks earlier than failed breeders. Length of shifts and number of foraging trips during incubation were the most distinctive variables to identify the difference between successful and failed breeders. A similar pattern was also observed for the King penguin *Aptenodytes patagonicus* when a later egg laying date resulted in longer incubation shifts and breeding failure (Weimerskirch et al. 1992; Jouventin and Lagarde 1995). Thus, attendance patterns as measured during this study may provide a useful tool for monitoring the availability of the major prey items in the foraging zone at least. The attendance patterns may be a variable which is particularly responsive to change since little penguins only visit ashore during dusk or darkness. Therefore a delay of a few hours in obtaining sufficient prey will delay by 24 hours arrival back at the colony to relieve a partner or to feed a chick.

4 The effect of pair fidelity and mate guarding in the breeding success of little penguins

4.1 Introduction

Birds in the process of pair formation can reunite with their partner of the previous year or change partners. Birds can also retain or change their nest sites. Changing partners is caused by death or disappearance of previous mate or through divorce, ie birds form new pairs even though last seasons' partner is alive and present in the colony (Williams 1996). Several hypotheses have been suggested to explain the adaptive value of divorce to the pair formation. These can be divided in two groups: active and passive choice (Black 1996). In the active choice, birds choose to change partners to gain a better mate and/or territory since they have failed last season with their partners. This is known as the Incompatibility Theory, or there is a chance for birds to improve breeding performance, the Better Option Theory (Coulson 1966; Ens et al. 1993). In the passive choice, changing partners is not an option and divorce occurs by accident (Black 1996).

There is some evidence that seabirds changing partners and nest sites will affect timing of breeding and will have a cost in the breeding performance. South polar skuas *Catharacta maccormicki* may be less successful at breeding when birds change partners (Pietz and Parmelee 1994). A similar pattern occurs in the kittiwake gull *Rissa tridactyla* in which newly formed pairs delay laying date by about 10 days (Coulson 1966). An experimental nest manipulation with Leach's storm petrel showed that mate fidelity is a function of nest fidelity (Morse and Kress 1984).

Although 90% of penguins retained the same partner in successive seasons, there is little evidence that nest and pair fidelity will improve breeding success of penguins (see Williams 1996). There is an obvious advantage to changing nest sites from the border to the centre which will improve breeding performance (Spurr 1975). In this case, nest location in the colony rather than nest fidelity is important to the breeding success. However, studies on pair fidelity in penguins so far have not considered the effect of age (Williams 1996). Breeding experience as a function of age does affect breeding performance in seabirds (Lack 1968; Ashmole 1971). Older seabirds start to breed earlier, produce more chicks and have a better hatching success (eg Croxall et al., 1992; Dann and Cullen, 1990; Nisbet et al., 1984). Therefore it was thought that age could also affect pair

fidelity. The present study investigated whether experience as a function of age and laying date interfere in the mate and nest selection of little penguins as these variables are important factors in the reproductive performance of seabirds.

The constant presence of males with their females in the colony during pre-egg periods has been reported as a strategy to strengthen pair bonding and territory defence (Birkhead and Møller 1992). This behaviour has been described for several species as 'mate guarding' when males guard their partner against cuckoldry and loss of paternity (Birkhead and Møller 1992). As mate guarding has not been reported for little penguins, this study examined whether little penguin males exhibit this behaviour and its possible role in the mating behaviour.

Males guard their partners but also try to copulate outside their partnership, ie try to have extra pair copulation (EPC). Females also display this behaviour which makes it an important mechanism for genetic diversity (Birkhead and Møller 1992). The Adélie penguin *Pygoscelis adeliae* is probably the only penguin in which EPC has been reported. Davis (1991) believed it happened only when birds switched partners in the season but Hunter et al. (1995) suggested that EPC is part of the pair bonding process. EPC, as an opportunistic behaviour, happens very quickly which makes it hard to detect in a penguin colony where the territory range is narrow. It is even harder to detect in little penguins which copulate mainly during the night and in burrows. In this study, observations of the penguin pairs in their burrows with different partners was used to suggest that extra-pair copulation occurs during the pre-egg period.

This chapter examines the reproductive cost to little penguins in changing partners or burrows. It also describes mate guarding for little penguins and speculates on the occurrence of extra-pair copulation during pre-egg periods.

4.2   Method

Little penguins used in this study were transponder birds from the Parade colony described in Chapter 2. The field procedures and statistics are also in Chapter 2.

Pair fidelity is defined as the percentage of birds in the present season reunited with their partner of the previous year. Pair fidelity was ranked in four categories: reunited, newly-united, widowed and divorced, and defined as:

Newly-united   first time recorded breeding in the colony.

Reunited   paired with previous season partner.

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Divorced   partner alive but breeding with somebody else.

Widowed   partner vanished, not even coming ashore as recorded by the APMS, probably dead.

The proportion of occurrence of each category was calculated as the number of events divided by the total number of pairs multiplied by 100.

Divorce in this study meant the end of a partnership and quoting D. M. Mock (in Black 1996): "No sane reader should misinterpret divorce in birds as implying legal dissolution of a marriage, with alimony and lawyers' fees".

Mate guard behaviour is when a male remains close to his female to assure his paternity as long as she is fertile. Mate guard ceases when she in no longer fertile (Birkhead and Møller 1992). Mate guard in this study was recorded by the frequency of male presence with its partner at laying period.

The sex ratio of birds with transponders was almost equal between male and female (1.00 : 1.05, $x^2_{230,\,1} = 0.11$, p = 0.790). This sex ratio was achieved randomly since birds, regardless of their sex, were marked with a transponder as soon as they were recorded in the colony.

Extra-pair copulation is when both males and females seek more than a single partner during a single fertile period (Birkhead and Møller 1992). Extra-pair presence (EPP) was used to indicate extra-pair copulation. Birds were scored as extra-pair presence (EPP) when they were observed before laying in their burrow, during day time, with a different partner, ie partner other than the definitive partner.

All analysis in this study was based on two seasons except for pair fidelity which was available for the 1996/97 season only since it integrates the events of two seasons.

4.3 Results

4.3.1 Pair fidelity

The divorce rate for 1996/97 was 28% which was higher than the 18% rate previously reported by Reilly and Cullen (1981) for Phillip Island (Table 4.1).

All reunited breeders were successful while a high proportion of newly-united breeders failed to breed successfully ($x^2_2 = 9.57$, p = 0.002). The proportion of success amongst divorced and widowed birds was similar to the ratio expected in the population for the 1996/97 season.

Table 4.1 shows the breeding success, based on the chick production, of the different categories of pair fidelity. The mean chick production for the 1996/97 season was 1.3 chicks per pair.

pair formation	% breeders	breeding success
Newly-united	28	0.9
Reunited	32	1.82
Divorced	28	1.31
Widowed	12	1.07

Table 4.1   Proportion of breeding birds according to pair fidelity categories and their breeding success expressed as number of chicks per pair in the 1996/97 season.

4.3.2 Age and pair fidelity

Age against pair fidelity was compared for 63% of birds which had known ages. Table 4.2 shows the mean age of different pair fidelity groups. Divorced and newly-united breeders were over two years younger than widowed and reunited breeders (ANOVA, $F_{3, 67} = 4.25$, $p = 0.008$).

pair formation	mean age (years)	sd	n
Newly-united	5.8	3.23	9
Reunited	8.1	3.47	29
Divorced	6.2	3.35	18
Widowed	8.4	2.61	11

Table 4.2   The mean age of the breeders according to the pair fidelity categories.

4.3.3 Pair fidelity and laying date

The mean laying date for newly-united pairs was 17 November 1996, about 8 to 11 days later than other pair fidelity groups (ANOVA, $F_{107, 3} = 3.96$, $p = 0.004$). Newly-united breeders laid eggs 11 days later than reunited breeders (Tukey-Kramer $p = 0.002$) and 8 days later than divorced breeders (Tukey-Kramer $p = 0.044$). Newly-united and widowed breeders had no significant difference probably due to the small sample size of widowed birds. This observation is the opposite of what was previously reported for little penguins, when newly-united pairs laid 21 days earlier (Reilly and Cullen 1981).

4.3.4 Previous season affecting next breeding season

A total number of 25 out of 27 successful breeders of the previous season also bred successfully in the next season whether they reunited or changed partners. Two widowed females failed to breed successfully.

In contrast, failed breeders from the previous season had a higher divorce rate than successful breeders in the next season (Table 4.3).

Successful breeders of the previous season tended to lay eggs 9 days earlier than failed ones ($t_{68} = 3.20$, $p = 0.002$). Within the pair fidelity groups, the difference of laying date was significantly earlier only in the reunited partner group when the previous season's successful breeders laid eggs two weeks earlier than failed breeders ($t_{32} = 4.31$, $p < 0.001$). In the other pair fidelity groups, previous year breeding performance did not affect the mean laying date of the next season.

| | Pair formation in 1996/97: | | | |
	reunited	divorced	widowed	divorce rate %
Failed in 1995/96	16	19	8	44
Successful in 1995/96	18	4	5	15

Table 4.3 **The effect of previous season breeding performance on the pair fidelity in the next season. The number of birds for each pair fidelity category is shown according to the breeding performance of the previous year. The proportion of divorce related to the total number of birds is also shown.**

4.3.5 Burrow fidelity

Reunited and widowed breeders have a higher return rate to the same burrow from the previous season than divorced breeders (Figure 4.1).
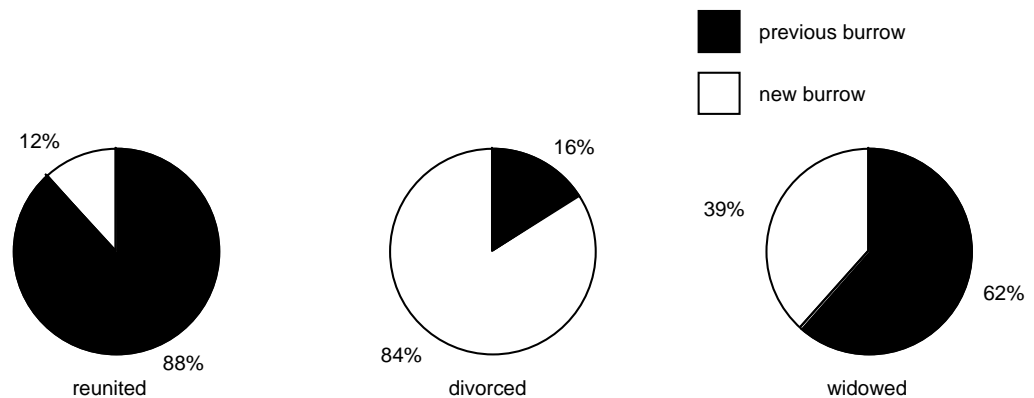
Figure 4.1 Proportion of birds returning to the same burrow relate to the pair fidelity categories.

A high percentage of birds (95%) which returned to their original burrows bred successfully. Only two widowed females failed even though they bred in the same burrow as the previous season. On the other hand, about 37% of birds which changed burrows failed to breed successfully; a higher percentage of failure than expected in the breeding

population ($x^2{}_2$ = 6.03, p = 0.01). Older birds (mean = 8.1 years old, sd = 3.17) returned to the same burrow and younger (mean = 6.5 years old, sd = 3.44) birds nested in a new burrow (t $_{65}$ = 2.77, p = 0.007, transformed data). This difference was significant when comparing young and old males (t $_{23.5}$ = 2.14, p = 0.042) but not in the female age group (t $_{34}$ = 1.71, p = 0.096). This suggests that competition for burrows is stronger in males and favours older males.

4.3.6 Mate guard

The daily presence of 103 males was recorded throughout two seasons. They tended to stay close to their females throughout the pre-egg period. Males were recorded more often in the colony during the courtship period, had shorter pre-laying exodus and consequently returned earlier for laying than females. After the pre-laying exodus; both male and female stay in the burrow before laying eggs.

About 88% of males departed to sea between two days before and five days after first egg was laid (Figure 4.2). As nests were checked for eggs once a day it is likely that males started to leave females unattended as soon as the first egg was laid. The second egg was laid about one day later and females stayed in the burrows for 2 - 3 days more incubating the eggs.
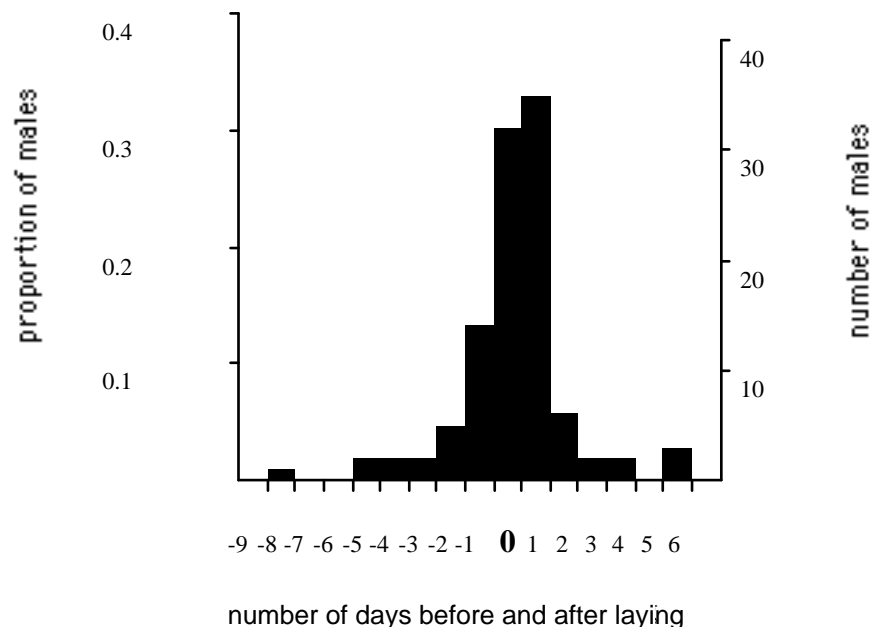
Figure 4.2 Histogram showing the proportion of males departing from the colony in relation to laying date of the first egg (day zero).

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Successful males in the 1995/96 season guarded their females almost one day longer than those males which failed to breed successfully (t_{52} = 2.34, p = 0.023). The pattern was similar in the following season but the difference was not significant. The timing of mate guard was not affected by pair fidelity and age. Young males with new partners had the same guard pattern as old males with same partners.

4.3.7 Sex ratio

In the sex ratio of birds coming ashore, number of males exceeded females over a total period of 26 months as recorded by the APMS (1.15 : 1, n = 14361, p << 0.001).

The number of males was significantly higher than females, at less than 0.05 level of significance, in 40% of the weeks while females exceeded males in only 6% of the weeks. Sex ratio was even in 54% of the weeks. Around courtship, male presence was always higher than females. Sex ratio was balanced after laying, throughout incubation and up to 2/3 of the chick rearing period. Males were in the majority again in the last 1/3 of the chick rearing period (Figure 4.3).
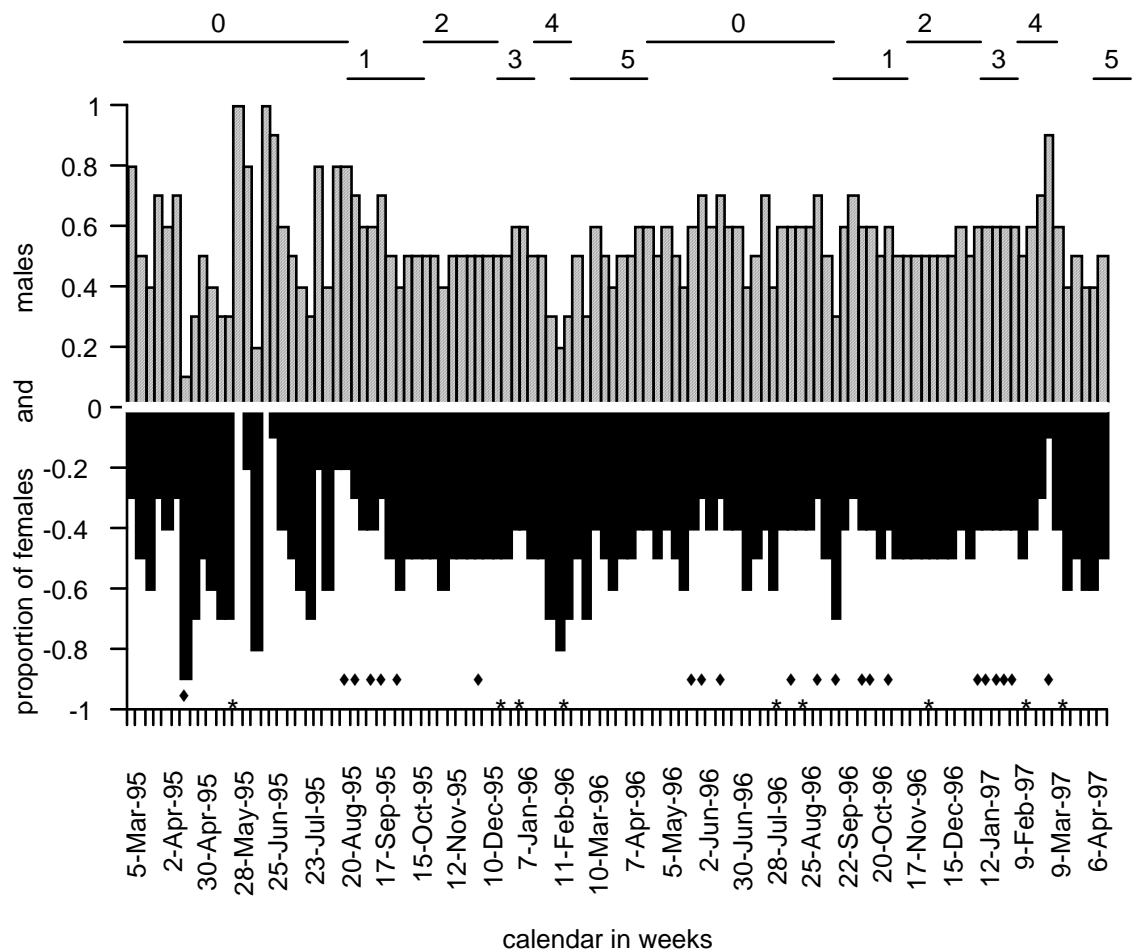
Figure 4.3 Sex ratio of birds ashore March 1995 to April 1997. The proportion of both males and females are represented in the y axis. Symbols at the bottom indicate the weeks that the sex ratio was significantly different at 0.05 (♦) and 0.01 (н) using chisquare. Life cycle is represented at the top in sequence of inter-breeding (0), courtship (1), incubation (2), chick guard (3), post guard (4) and moult (5).

4.3.8 Extra-pair presence

Extra-pair presence (EPP) was used as indication of extra-pair copulation, eg birds seeking different partners. Birds were scored as extra-pair presence (EPP) when they were found in the burrow before laying date with a partner other than the definitive partner of the season. This behaviour was performed by males and females and it was common during courtship but rare on laying period.

About 33% of breeding birds were recorded EPP at the same stage of both seasons. In the 1995/96 season, 25% of the birds were 1 out of 13 days in the burrow with a different partner, eg 13 days with the definitive partner and 1 day in the presence of a different partner. In the 1996/97 season, 41% of the birds were 1 out of 9 days in the burrow with a different partner.

For the 1996/97 season, all pair fidelity categories except newly-united had similar average days on EPP (mean = 1.21 days, sd = 1.59, n = 75). Newly-united breeders had fewer extra partners than other pair fidelity groups (mean = 0.44, sd = 0.93, n = 27). Indeed, only 6 birds out of 27 newly-united breeders were recorded on EPP. However, no great value is attached to this finding since these birds could have been with different partners outside the study area and this may have underestimated their frequency of presence and frequency of EPP as well.

The frequency of extra-pair presence behaviour did not correlate with breeding success, sex, age, courtship length and mate guard.

4.3.9 Individual cases of pair bonding

Behavioural ecology assumes that selection operates at the level of the individual, which will determine differences in breeding success (Birkhead and Møller 1992). So far this study combined the results of different individuals and calculated mean values, glossing over individual effects. In this section some cases of individual birds performing particular pair fidelity behaviour are reported.

Burrow I had two females (A and B) involved with one male (C). Female A paired with male C and laid two eggs. But female A's last year partner (male D) returned and she moved into Burrow II with him and she deserted her eggs in Burrow I. Female B took over the eggs from Burrow I and, shifting in with male C, incubated and fledged two chicks from female A's eggs. In Burrow II, the same burrow as the last season, female A laid more two eggs and fledged two chicks together with male D.

A similar situation occurred in another burrow with again two females (A and B) and one male (C). Female A laid two eggs and female B, which arrived later, also laid two eggs in the same burrow. Female A and male C incubated four eggs but only one hatched and eventually one chick fledged. Female A paired with another male much later on in the season in another burrow and failed to breed at all.

In another case, male C was involved with two females A and B in two different burrows. Both females laid two eggs but the male only incubated the eggs from female A in her burrow. Female B deserted its eggs and tried to breed with another male without success.

An inverse situation, two males (C and D) competed for the same burrow and only one female (A). Male C paired with female A during courtship in Burrow I and both returned to the colony on the same day of the laying period. Male (D) turned up two days after and sat alone in a nearby nest (Burrow II) staying there until two days after female A laid the first egg. At the middle of incubation of pair AC, male (D) took over Burrow I and sat on their eggs. Male C could not return to his original burrow (I) when back in the colony and moved into Burrow II. These males were observed fighting for over 9 nights consecutively without leaving the colony. After this period, which is much higher than the average incubation shift of 3.1 days (Chiaradia and Kerry in press), both males left the colony for the sea. Female A returned and finished incubation and hatching but none of the males returned to relieve her. She spent 8 days guarding their chicks in contrast to 1.2 days average for chick guard period (Chiaradia and Kerry in press). Male C returned on day 8 after hatching. Chicks were found squashed in the burrow at day 9. Male D and female A reunited in Burrow I about two weeks later for a second clutch. They incubated the eggs in an unusual two long shifts each and chicks were dead two days after hatching.

In summary, two females can compete for one male and vice-versa which also involves competition for a burrow. These cases show the wide range of pair bonding behaviour

and illustrate the cost involved for individual birds in changing partners within the season.

4.4 Discussion

The data show that little penguins are socially monogamous but sexually promiscuous as males guard their partners and both sexes are involved in extra-pair activities. About 68% of breeding birds changed partners through divorce, death or disappearance of previous season partner. Individual cases of pair bonding illustrated how birds compete for partners and burrows. The question which remains is on the relative adaptive value of reuniting or changing partners and burrows and whether this behaviour can affect breeding performance.

4.4.1 The effect of pair and burrow fidelity on breeding

One reason why little penguins divorce or reunite with previous year partner is probably associated with the breeding timetable (Table 4.4). For birds, breeding onset needs to be timed on the availability of food for the young (Lack 1968). A model on the chronology of food resources suggests that the temporal variation between resource availability and resource demand will determine the most favourable breeding time (Wittenberger and Hunt 1985). Successful little penguin breeders laid eggs about two weeks earlier than failed breeders which was highly significant for both seasons ($p < 0.001$). This pattern reflected in the pair fidelity groups. Newly-united breeders laid eggs 8 to 11 days later than other pairing groups. Within the reunited breeder group, previous year successful breeders tended to lay 9 days earlier than ones which failed last season. Previous work reported that new breeders laid eggs about 21 days earlier than reunited pairs (Reilly and Cullen 1981), which is a very different perspective from that found in this study. However, Cullen (pers. comm.), analysing his data from years subsequently after Reilly and Cullen (1981), showed that new breeders laying is delayed by about 10 days which agrees with 8 to 11 days reported for this study. Indeed, it seems that little penguins need to make an effort to start to breed as early as possible to breed successfully. For little penguins at Phillip Island it is clear that successful breeders start to breed on average two weeks earlier than failed breeders (Chapter 3). Foraging conditions in the region deteriorated from the middle to the end of both breeding seasons when duration of foraging trips increased and growth of chicks reduced regardless their age (see Chapter 5). To prevail in this race against time, returning to the same burrow and

reuniting with the same partner was the strategy adopted by successful breeders. They produced more chicks to fledging than breeders which changed burrows and partners.

Another reason which may influence pair fidelity is the age of the birds (Table 4.4). Considering that little penguins breed every year, age was assumed equal to breeding experience (Dann 1992). Experience affecting breeding success, which has been reported for several seabirds including little penguins, is not a new theory (Lack 1968; Ashmole 1971; Nisbet et al. 1984; Dann and Cullen 1990; Croxall et al. 1992b). This study showed that experience affected pair fidelity which therefore affected breeding success. Birds which reunited with the same partner were two years older than birds which divorced or formed new pairs, ie reunited breeders were two seasons ahead in experience compared with divorced and newly-united breeders. Widowed breeders were as old as reunited breeders but they had their breeding performance reduced by probably being forced to change partners. Some newly-united breeders could be divorced birds which were breeding outside the study area in the previous season. Older birds seem to have the experience to reunite with their partner which saved them time on mate sampling. They could start to breed earlier than younger birds which need first to find and then probably fight for a new partner. Additionally, older birds also tended to return to the same burrow as the previous year, which was significant for males but not in females. This may also help their breeding performance since 95% of birds which returned to their old burrow bred successfully.

variable	success	failure
Age	Older	Younger
Pair fidelity	Reunited	Changed
Burrow selection	Old	New
Onset of breeding *	Earlier	Delayed
Laying period *	Synchronism	Asynchronism

Table 4.4 **The effect of pair fidelity and breeding timetable in the breeding success of little penguins. Variables on onset of breeding and laying period (*) are from Chapter 3.**

4.4.2 *The benefit of divorce behaviour*

The little penguin is reported to have the lowest divorce rate of the penguins (Reilly and Cullen 1981; Williams 1996). In this study, however, the divorce rate of 28% was higher than the 18% previously reported for little penguins by Reilly and Cullen (1981) at the same location. They calculated divorce rate, in a different way from this study, by

the number of divorced breeders divided by the sum of divorced and reunited breeders. Recalculating the present data using Reilly and Cullen's method, the divorce rate jumped to 47%. Nevertheless, Cullen (pers. comm.), analysing his data from later years after Reilly and Cullen (1981), found a divorce rate ranging from 17 to 42% (average 26%) with higher rates following a season of low breeding performance. The finding in this study agrees with Cullen's latest unpublished data. Thus, the little penguin has probably one of the highest divorce rates amongst penguins and not the lowest as previously thought .

Consecutive pair reunion recorded for 11 years in little penguins and for 13 in yellow-eyed penguins illustrates a trend for pair fidelity in penguins (Richdale 1957; Reilly and Cullen 1981). Little penguins may have evolved to be faithful to their burrow and mate in order to breed successfully (Table 4.4) so why divorce when reuniting with the previous partner apparently guarantees a successful breeding season?

Little penguins breed in a unpredictable environment with a highly varied inter-seasonal breeding onset (Reilly and Cullen 1981; Stahel and Gales 1987; Wooller et al. 1991). Their high mortality rates may prevent birds from waiting very long for their partners to return (Black 1996). Thus, synchrony at pair formation may not happen every year so breeding with the same partner in consecutive seasons may not be possible for little penguins to adopt for life. Other penguin species seem to maintain pair fidelity for three to four years which could terminate mainly by death of the partner, with divorce as only a secondary factor (Williams 1996). Theoretically there is a long term benefit to divorcing. Breeding success should be low when birds divorce but it can be improved in the next seasons (Ens et al. 1996). Little penguins, however, have a short breeding life of about 3 to 4 years (Dann and Cullen 1990) and they probably can not afford to sacrifice a season by changing partners. This study, based on two breeding seasons, does not allow a critical view of this life-long trend. Nevertheless, it provides evidence that divorce is more common in the earlier years of breeding and it may be just a by-product of young birds losing territory which means they are unable to keep pair bonding. Based on this result divorce behaviour has no obvious benefit for little penguins but only further long term studies would confirm whether little penguin can be included in the hypothesis group that divorce is a passive choice.

4.4.3 Mate guard and sex ratio

Males followed their partners in the colony throughout courtship and pre-laying. Females were found alone as soon they laid the first egg which suggests that males were not only defending their territory but guarding their females as well. Mate guarding behaviour is associated with males minimising the risk of losing paternity when their partners are fertile. Males try to spend as much time as possible close to their females and the proportion of this time is one way to measure mate guard (Birkhead and Møller 1992). Little penguin males in this study showed consistent mate guarding behaviour regardless of their age and breeding success. This suggests that little penguin male guards his partner until he is assured that eggs are laid which could also be the signal to go foraging and to prepare for his first incubation shift.

Males come ashore more often during courtship, pre-laying exodus and laying when they are engaged in different activities from females (Chiaradia and Kerry in press). Reilly and Cullen (1981) recorded that males were present more often than females from moulting to laying. Indeed, it was observed that the number of males ashore exceeded females 40% of the time. A higher male presence was concentrated during courtship in both breeding seasons though this pattern was more evident in the 1996/97 season. This agrees with the theory that there is a surplus of males in the colony before laying (Reilly and Cullen 1982; Williams 1996). Males managed to be the majority even though the sampling population had an even sex ratio. This suggests that male surplus is probably related to male behaviour of mate guarding and nest defence rather than an unbalanced sex ratio.

4.4.4 Extra-pair presence (EPP)

Mate guarding behaviour and surplus of males before laying provided evidence that little penguins are involved in extra-pair copulation. In fact, about 33% of breeding birds were recorded in the burrow with a different partner before laying, labelled as 'extra-pair presence' (EPP). Burrow nesting little penguins can copulate outside and inside the burrows which makes it difficult to observe and measure precisely the frequency of copulation. However, some preliminary observation on mating behaviour showed that little penguins, regardless of their sex, can copulate with up to four different birds in one night (Emma Cunningham, pers. comm.). Extra-pair presence was assumed then as indication of extra-pair copulation.

The rate of EPP, based on daytime presence, may have been underestimated since little penguins' social life takes place at night when copulation is likely to happen. Although EPP does not confirm that birds had copulated, it lends support to the assumption that extra-pair copulation occurs in little penguins and probably more often than 33% of the EPP rate.

No correlation was found between days of EPP and breeding success. Similar to extra-pair copulation, EPP is probably an opportunistic behaviour and birds may have priorities over seeking extra-pair copulation (Birkhead and Møller 1992). Little penguin males, for instance, may concentrate their efforts on mate guarding and ensure paternity of their off-springs before adventuring into extra-pair copulations.

EPP was common during courtship but rare in laying period. For little penguins, the period between courtship and laying has an interval of about 10 days which may be enough for males to guard their partners and prevent cuckoldry. It is not clear when penguin eggs are fertilised but there is evidence for Adélie penguins *Pygoscelis adeliae* that it could happen from 7 days to one day before laying (Astheimer and Grau 1985). Although females can have multiple copulation, last-male sperm is probably responsible for the fertilisation (Williams 1996). DNA fingerprinting on royal penguins *Eudyptes schlegeli* found a 7% rate of extra-pair paternity (C. St. Clair in Williams, 1996). Assuming that EPP is a good indication of extra-pair copulation, lost paternity may be low for little penguins as well since the EPP was not common at laying. Whether extra-pair presence correlates with extra-pair copulation and, indeed, with extra-pair paternity in little penguins could be only tested in further studies using molecular techniques.

5 Chick rearing period: the effects of chick provisioning and chick growth rates on the breeding performance of little penguins *Eudyptula minor* in years of high and low breeding success[4]

5.1 Introduction

Low annual reproductive output and slow chick growth in seabirds suggest severe limitations on food resources have shaped the birds' breeding strategy (eg Lack 1968). During their chick rearing period, breeding penguins have a limited foraging range since they have to feed themselves and provide meals at regular intervals to their chicks (eg Culik 1994; Kerry et al. 1997). Gales and Green (1990) showed that chick rearing is the most expensive period in terms of energy in the life cycle of little penguins. Birds expend 31% of their annual energy budget to rear chicks although this period represents only 16% of the time in their annual cycle. This period is likely to be the most sensitive period in the breeding cycle to variations of food supply. A reduction of prey abundance could result in an increased effort by adults to breed and consequently, decreases in chick growth rates and breeding success (Uttley et al. 1994). Such effects will depend on a number of factors including the time that birds allocate to forage to sustain themselves and their chicks and their tolerance to temporal changes in food supply (Williams and Rothery 1990). Several studies have characterised good and poor breeding performance by little penguins based on chick production (eg Hodgson 1975; Dann and Cullen 1990; Wooller et al. 1991; Dann 1992), but few have examined how birds adjust their breeding effort in terms of length of the chick rearing period and chick growth rates in response to intra-annual fluctuations of food supply.

A classical discussion on seabird foraging ecology is whether the variation in meal mass brought by the parents is a response to changes in the demands of the growing chick or to variations in food availability (see Bolton 1995). If the meal mass is limited by availability, a distinctive difference in food delivered to chicks between good and poor reproductive years would be expected (Cairns 1987). In the little penguin, inter-annual variations in food availability appear to have influenced the date of the onset of breeding, with breeding starting earlier in years when food availability is high (Hobday 1992). Chapter 6 will examine whether little penguins vary their prey depending on the

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[4] Chiaradia, A. and Nisbet, I. C. T. (2006). Plasticity in parental provisioning and chick growth in Little Penguins *Eudyptula minor* in years of high and low breeding success. Ardea 94(2): 257 - 270.

age of their chicks. In this chapter, I investigate whether chick provisioning rates are set by the demand of the growing chick, or by food supply, and calculate the total food consumed by the chicks.

Foraging trip duration may change during the breeding season, perhaps reflecting changes in how far a bird has to travel to find food and in turn reflecting prey availability (Cairns 1987; Monaghan et al. 1994). Rothschild (1977) suggested that investigations of foraging trip duration could indicate prey availability in a similar manner as does catch per unit effort in fisheries' models.

Previous studies of the duration of foraging trips of little penguins at Phillip Island have concluded that birds forage at different distances from the island at different times of the year (Weavers 1992; Collins et al. 1994). These studies measured the distances travelled by penguins that carried back-mounted radio transmitters. This method has several short falls, including: tracking is discontinuous, only small sample sizes can be used and the instruments may affect the birds' foraging performance (eg Gales et al. 1990). Hence, although providing useful information on where the penguins might need to go to find food, radio tracking may not provide robust data on prey availability. A better measure of prey availability may be foraging trip duration, provided the means of measuring this are non-invasive. In this study, transponders implanted under the penguins' skin combined with an automated penguin monitoring system (APMS) were used to examine fluctuations in the foraging trip duration of little penguins over the post guard period. This method enables large sample sizes which are required to detect changes in food availability (Croxall et al. 1988).

This chapter investigates temporal changes in chick provisioning, which includes meal mass that parents delivered to their chicks and adult foraging trip duration, and chick growth rates during two breeding seasons. It was possible to compare these variables during years of high and low numbers of chicks fledged, i.e. years of large difference in breeding success. In 1995/96, a mean of 0.3 chicks fledged per breeding pair while in 1996/97, 1.3 chicks fledged per breeding pair. These rates compare with an average rate over 20 years of 0.8 chicks per pair (Dann and Cullen 1990, for years 1967 to 1988). The comparison between a good and a poor year enabled to investigate the influence of these variables on breeding success.

5.2   Method

The field work routine and statistical analysis used in this chapter are described in Chapter 2, method.

The length a chick was reared was measured from the date of its hatching until it fledged. Hatching was determined by inspecting nests at intervals of one day and fledging was the date when chicks went to sea. The chick rearing period was divided into guard, when one parent remained with the chick and post guard when chicks were left unguarded at the nest so both parents could forage.

Chick weighing started at the end of the guard period to avoid disturbance to the adults. Chicks were weighed to ±1 g using a digital balance, twice a day until fledging.

Weighing times were early in the morning (about 8:00am, Eastern Standard Time - EST) and early evening (between 6:00pm to 8:00pm EST). Chicks were always weighed in the same order. These times were at least 2 hours from when chicks would have been fed, which would be when parents arrive home at 9pm to 11pm.

A single day experiment was conducted to determine the rate of body mass loss by the chicks, so that chick mass immediately prior to feeding could be estimated. Fifteen chicks at different ages were weighed hourly for a period of 17 hours between feeding times and then the proportion of body mass loss was calculated. The difference of body mass among clusters of hours was tested using ANOVA nested by hours. Chick weights were then regressed against time of day to obtain a correction factor that enabled the prediction of a chick mass immediately prior to feeding. It was assumed that at 11pm all chicks that had been fed that night had received their meal. Therefore 11pm was used as a constant feeding. The corrected weights were used in the analysis of meal mass delivered to the chicks.

Chicks were individually identified using non-toxic dye and numbered Velcro™ bands, each 10 mm wide and 50 mm long. Chicks were dyed after hatching and fitted with a band at the beginning of post guard. At first the bands were fitted on the chick's leg, but they were moved to the flipper when chicks were more developed. The bands proved to be an efficient marker but should be used with care. Two chicks developed swollen feet but the swelling disappeared in the hours after the strip was removed. This problem was minimised by checking the chicks twice a day.

The foraging trip duration (in days) was obtained from birds with transponders that had their visits to the colony recorded by the APMS (see Chapter 2).

Foraging trip duration and meal mass at post guard were analysed according to both time (calendar date) and chick age.

Because the timing of events, such as first chick hatched, varied between years, a standardised time scale had to be developed to enable inter-annual comparisons. To do this, the date of the first recorded post guard chick in each year was called day one for that year.

An estimation of food consumed by the Phillip Island population was calculated for both breeding seasons. Using a mean daily corrected meal mass multiplied by the age of each individual chick, the total mass received during post guard by both chicks that fledged successfully and chicks that died before fledging was calculated.

A descriptive analysis of the sea surface temperature (SST) in Bass Strait was based on compiled SST images produced by the CSIRO[5] Marine Research, Australia for the period of 1990 to 1997 (Cresswell 1997). This period is contemporaneous with the period of this study.

Chick body mass, meal mass and adult foraging trip duration were sampled daily but are presented in averages per week. This procedure was executed to smooth value-to-value aberrations and to present the relationships more clearly (Wilkinson 1989).

5.3 Results

Little penguins have a long laying period which results in a non-synchronised breeding season. Young and old chicks can be observed in the colony at the same time in the season. Since chick age did not necessarily correlate with the calendar date, the foraging performance against both time and chick age was analysed.

A time scale was used to allow the comparison of both breeding seasons at calendar date which had a lag phase of 4 weeks (Figure 5.1).

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[5] Commonwealth Scientific and Industrial Research Organisation
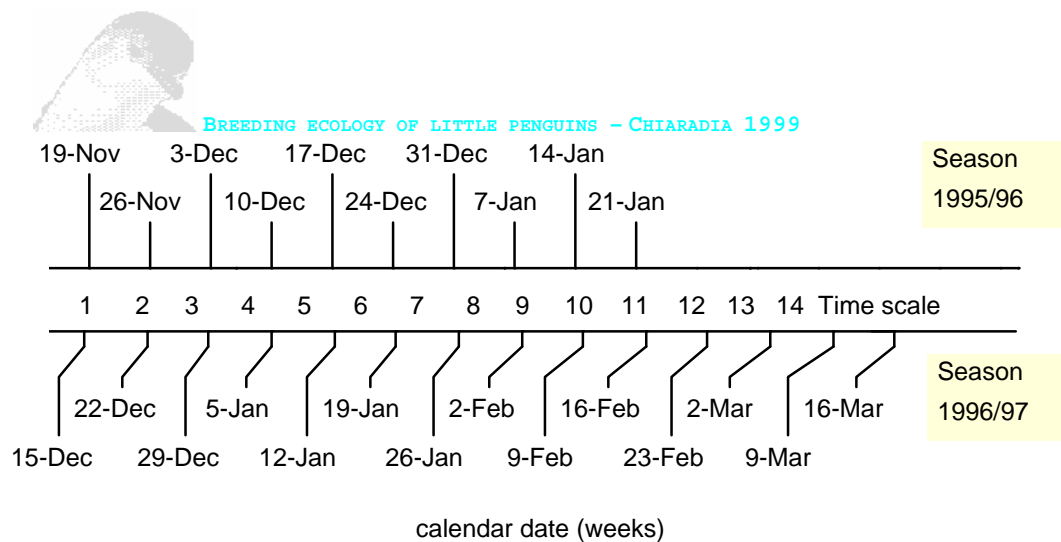
Figure 5.1 **Time scale used to compare post guard periods between two years where the second year exhibited an approximate lag phase of 4 weeks. Week one in the time scale represents the date when the first breeding pair ended the guard period, i.e. both parents went to sea and chicks were left alone in the burrows.**

5.3.1 Duration of chick rearing period

The chick guard period in 1995/96 (15.3 ± 3.3 days, n = 19 pairs) was significantly shorter than it was in 1996/97 (20.9 ± 5.5 days, n = 40 pairs, t_{56} = 4.14, p < 0.001). In contrast, the post guard period in the 1995/96 (50.5 ± 9.2 days, n = 19 pairs) was significantly longer than it was in 1996/97 (41.7 ± 9.3 days, n = 38 pairs, t_{55} = 3.35, p = 0.001). As a consequence, the chick rearing period in 1995/96 (65.7 ± 8.5 days, n = 19 pairs) had the same duration as in 1996/97 (62.1 ± 6.8 days, n = 38 pairs, t_{55} = 1.71, p = 0.092).

There were no differences between years in length of the chick rearing, guard and post guard periods for failed breeders. This result is probably due to the huge standard deviations and the small number of failed pairs in 1996/97 so the power of the t test was not sufficiently robust.

Although chicks fledged at a mean age of 9.1 ± 1.1 weeks (n = 2 years, max = 11 weeks), chick activity at calendar date in the colony, from first egg hatched to last fledging chick, lasted 12 and 16 weeks in the two years, respectively. Thus the colony chick rearing period was from 1 to 5 weeks longer than the longest individual chick rearing period.

5.3.2 Chick growth curve

Some 6389 weights based on 114 chicks were recorded for both breeding seasons; 2120 weights in the 1995/96 season and 4269 weights in the 1996/97 season. Overall, chicks received 211 grams of food on average per day.

Chick body mass was plotted against age to investigate growth rates. Weights were taken in the late afternoon prior to chicks being fed and therefore were the lightest measurements in the day. The growth curves for chicks that fledged were almost identical between breeding seasons, although chicks in 1996/97 were always heavier (two way ANOVA $F_{9, 1964} = 2.34$, $p = 0.013$). They reached their peak one week earlier than did chicks in 1995/96 (Figure 5.2). The chicks reached their peak body masses of 825g and 910g on average in 1995/96 and 1996/97 respectively after 6 and 7 weeks of growth, respectively. After achieving these masses, the chicks lost 150 to 200 grams on average prior to fledging (Figure 5.2).
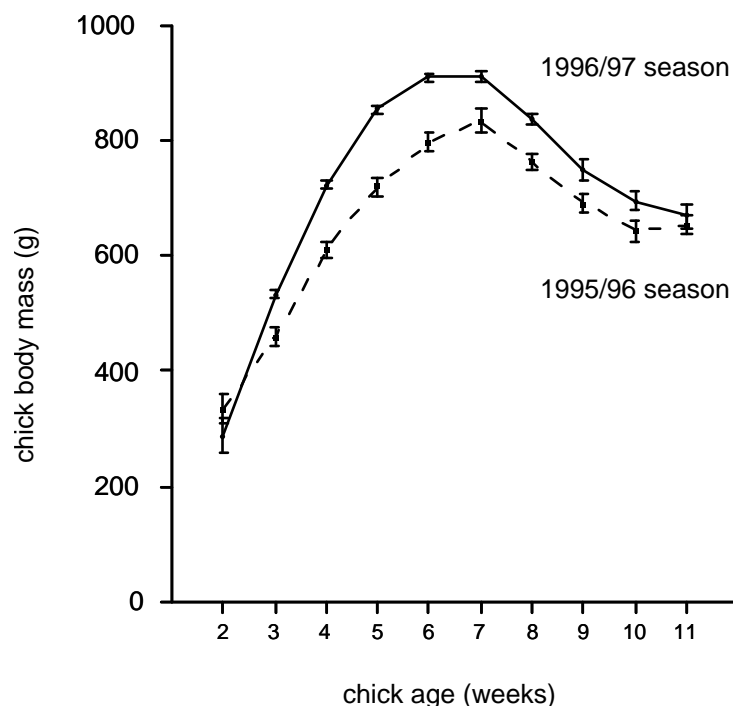
Figure 5.2   Chick growth curves of little penguins in two breeding seasons. Values are plotted for the post guard period. Only chicks that fledged are represented in the curves.

About 70% of chicks fledged between weeks 8 and 9 with the remainder between weeks 9 and 11. Those chicks fledging between weeks 9 and 11 were lighter than those

fledging between 8 and 9 weeks, producing a decrease at the end of the growth curve (Figure 5.2). Chicks that achieved body masses greater than 800g were able to fledge successfully, whereas chicks that did not pass the limits of 600g in 1995/96 and 700g in 1996/97 invariably failed.

Most fledging chicks received a meal in the night of fledging. In several burrows, both parents were present during daytime, probably resting, following the night that their last chick fledged. This observation accords with the argument that parents do not desert their chicks at the end of chick rearing (Burger 1980).

5.3.3 Corrected weights: standardised evening and morning weights

A chick could have its food provision delivered by one or both parents in the same day. No attempt was made to identify when this happened and therefore meal mass is related to the total mass received per chick per day.

Chicks that were weighed hourly lost weight at a rate of 1.1% per hour with no significant difference amongst hours (ANOVA nested design $F_{13, 10} = 2.75$, $r^2 = 0.902$, $p = 0.219$). Thus, a constant rate of body mass loss was assumed to correct the masses that were recorded during sampling. The corrected weights were calculated using the equations:

1) $Wc = Wi - \{Wi * (t_0 - t_1) * 0.011\}$ (before feeding, afternoon weights)

2) $Wc = Wi + \{Wi * (t_1 - t_0) * 0.011\}$ (after feeding, morning weights)

Where:

Wc corrected weight

Wi weight at sampling time

t_0 constant feeding time: 11:00pm EST

t_1 sampling time

0.011 constant weight loss rate

These two equations regress the weight to the feeding time. This correction was only used on chicks that had been fed. The balance between morning and evening weights provided a 'closer to real' meal size received by the chicks.

5.3.4 Meal mass fed to the chicks

There were variations over time in the meal mass delivered to the chicks (ANOVA, $F_{1968, 9} > 4.57$, $p \ll 0.001$, Figure 5.3). Mean meal masses increased from week 1 to week 5/6 and decreased sharply from week 6 to week 10 (Figure 5.3).

In 1995/96, penguins delivered lighter meals to their chicks over the first 5 weeks ($F_{4, 1325} = 2.54$, $p = 0.038$) then similar meal sizes were delivered between weeks 6 and 10 ($F_{4, 643} = 1.44$ and $p = 0.220$), when compared with the penguins in 1996/97. Similarly, chicks that eventually fledged had lower meal mass in the first 5 weeks of the 1995/96 chick rearing period than in the comparable period in 1996/97 ($F_{9, 1570} = 2.53$, $p = 0.007$). There was no between year difference in meal mass delivered to chicks that died prior to fledging ($F_{5, 379} = 0.38$, $p = 0.862$)
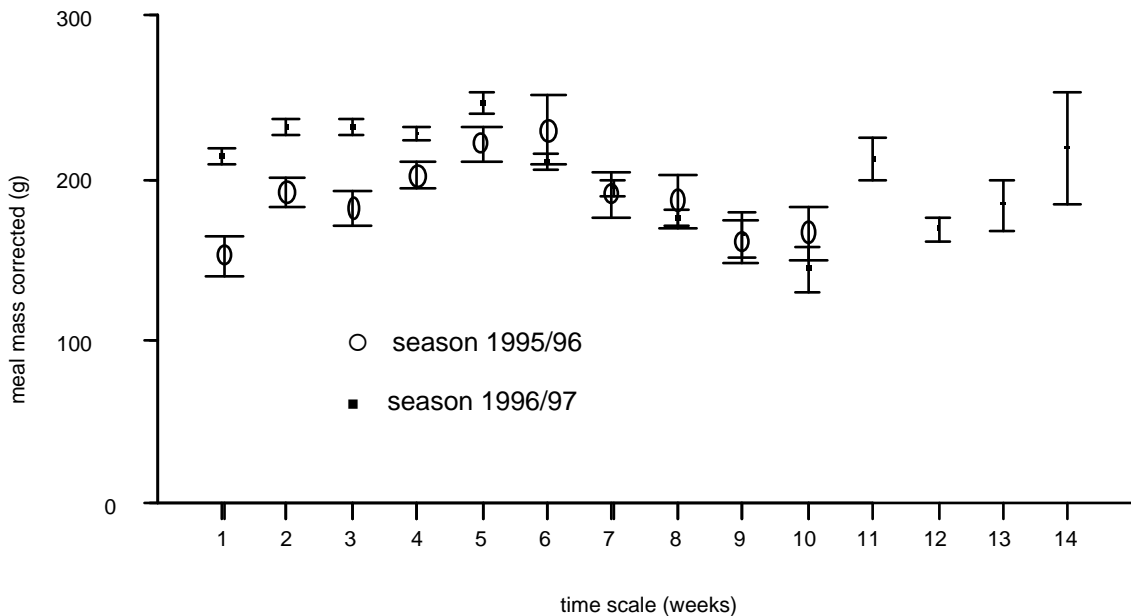
Figure 5.3 Variation of meal mass received by all chicks in both breeding seasons during post guard period. Time scale was used to compare two breeding seasons with a lag phase in the calendar date as explained in Figure 5.1. Data were collected daily and are presented in averages per week. Meal mass was corrected to regress the mass to the feeding times (see text).

In the chick age-specific analysis, the mean meal mass delivered by the parents increased for chicks of 2 to 6 weeks old with significant difference between breeding seasons ($t_{46 \text{ to } 355} > 2.60$, $p < 0.023$, Figure 5.4). Over this period, chicks in the 1996/97 season received on average 35 g more food per day. In chicks aged between 7 and 11

weeks, meal masses decreased ($F_{4, 541} = 4.09$ and $p = 0.003$) but this was not significantly different between breeding seasons ($F_{541,4} = 0.49$, $p = 0.746$).
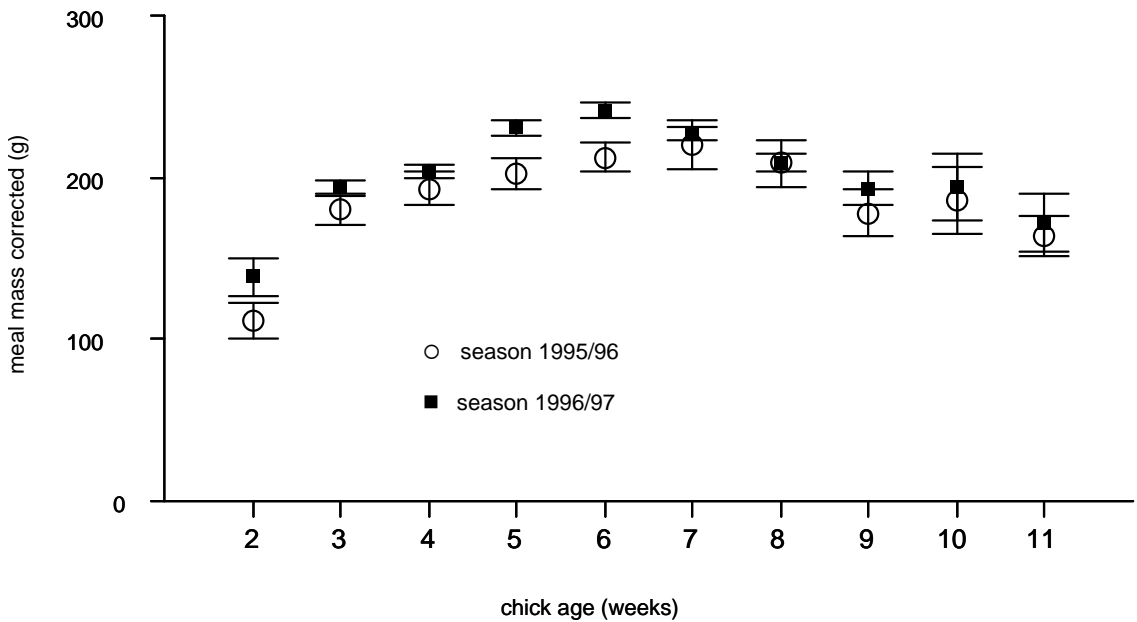
Figure 5.4 **Variation of meal mass received by all chicks in both breeding seasons related to the age of the chick. Data were collected daily and are presented in averages per week.**

The trend that chicks between 2 to 6 weeks of age from season 1996/97 received heavier meals than did the same aged chicks in 1995/96 was not observed when fledging ($F_{9, 1559} = 0.53$, $p = 0.853$) and failed ($F_{7, 429} = 1.74$, $p = 0.098$) chick groups were compared separately (Figure 5.5).
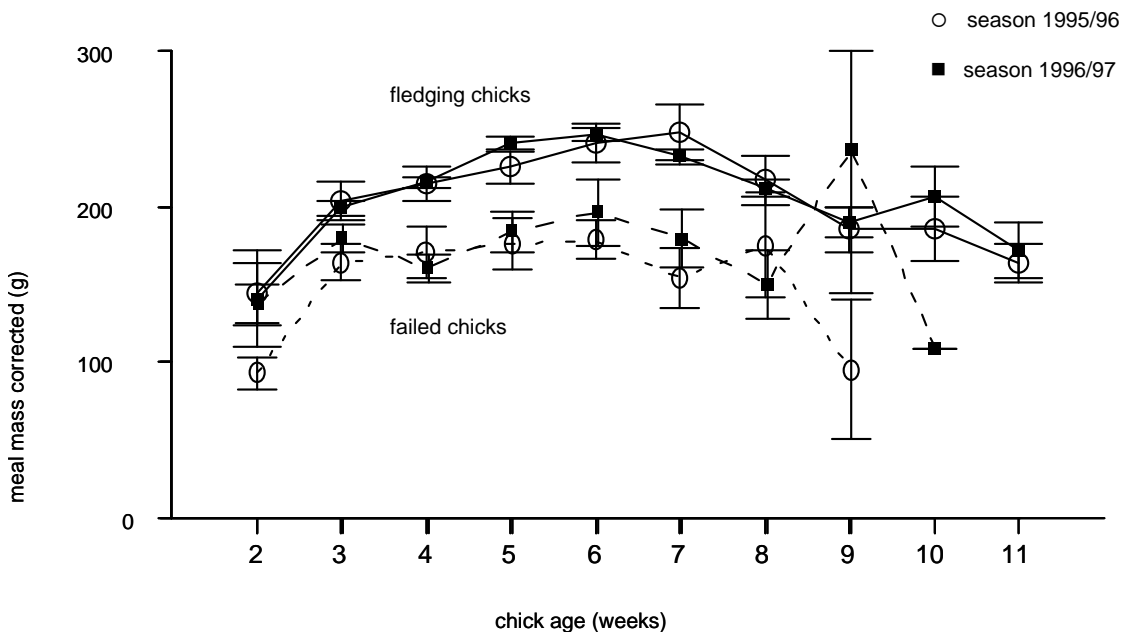
Figure 5.5 **Meal mass delivered to chicks that fledged (continuous lines) and those that failed to fledge (broken lines) in both breeding seasons related to the age of the chick. There was no inter-annual difference in meal sizes delivered to successful chicks.**

Figure 5.6 compares the chick body masses and the meal masses delivered by the parents according to the age of the chick. Both variables fluctuated similarly suggesting that the meal masses delivered were as response to the growing chick.
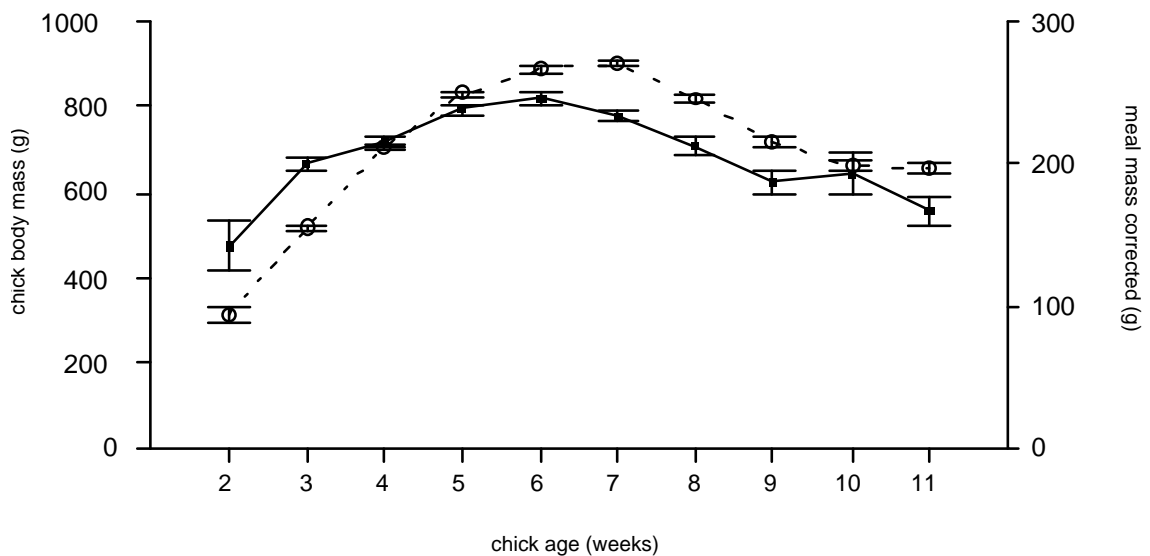
Figure 5.6 **The growth of the chick in relation to the meal mass delivered by their parents. Both chick body mass (continuous line) and meal mass (broken line) are presented in weekly averages according to the age of the chick.**

5.3.5 *Foraging trip duration of breeders at post guard*

A total of 2562 foraging trip durations was recorded for parents of post guard-aged chicks; 907 trips in the 1995/96 season and 1655 trips in the 1996/97 season. There were no substantial differences between foraging trip duration relative to time and the durations relative to chick age. However, both sets of data are presented to enable future comparisons.

The duration of foraging trips increased according to the calendar date in both breeding seasons (Figure 5.7). Breeding birds travelled between one to two days on average in the first 5 weeks increasing to two to three day trips from week 6 to the end of chick rearing. These patterns were different between breeding seasons and between successful and failed breeders.

Breeders in the 1995/96 season made longer trips on average than did breeders in the 1996/97 season (Figure 5.7). In the first season, foraging trip durations were longer than two day trips after week 3, increasing to 4 day trips in week 10. In the 1996/97 season, breeders kept their trip duration under the two-day average until week 10, by which time more than 70% of chicks had fledged (Figure 5.7).
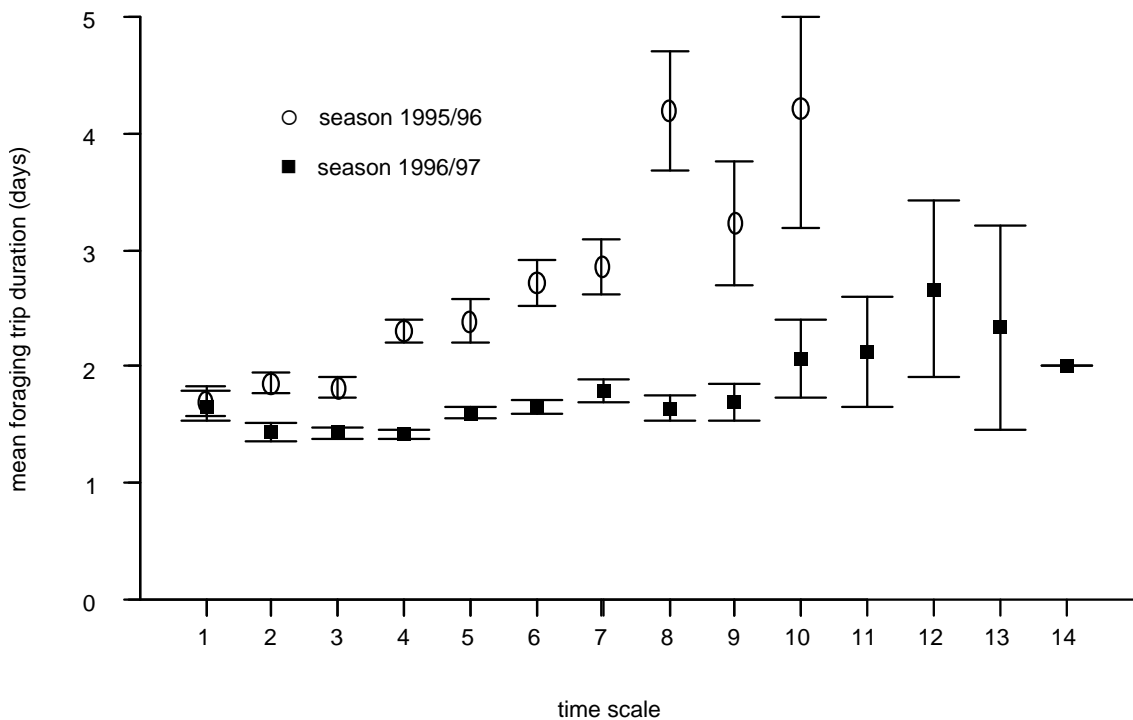
Figure 5.7 **Variation of foraging trip duration in both breeding seasons during post guard period in calendar time. Two years of data are compared on a standardised time scale (see Figure 5.1). Data are presented in averages per week.**

Using only successful parents in the analysis, birds from the 1995/96 season made longer foraging trips ($F_{9, 1952} = 2.14$, $p = 0.024$, Figure 5.8). There was no significant difference between female and males within each breeding season.
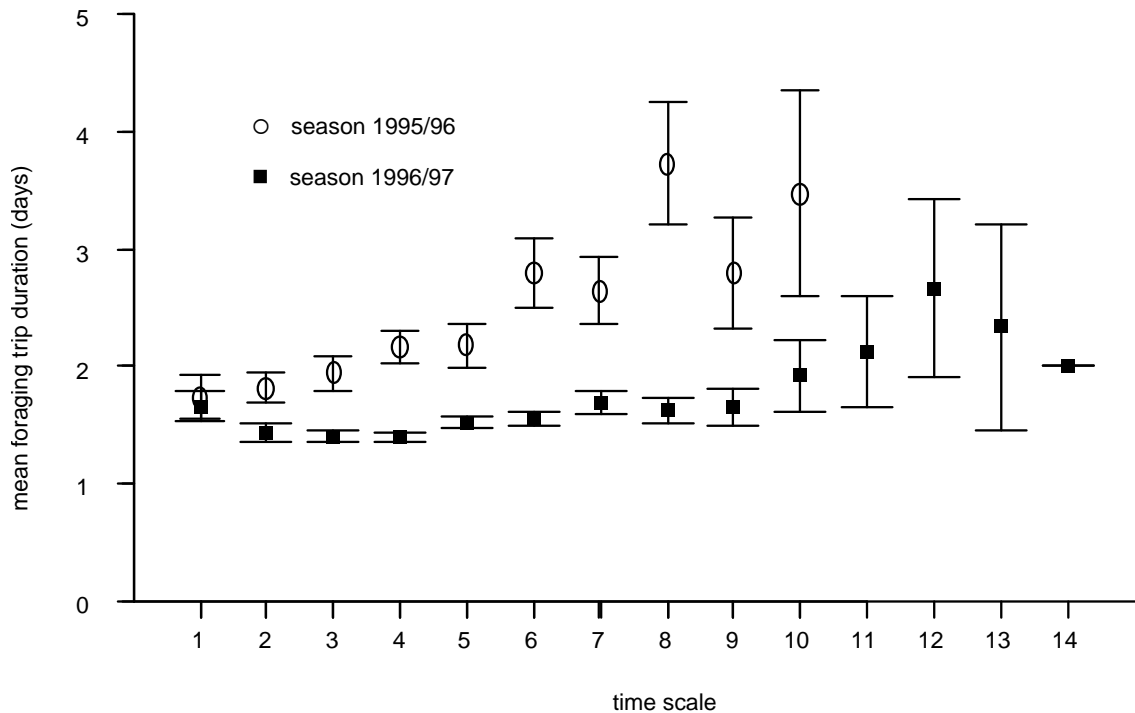
Figure 5.8 Foraging trip duration of successful breeders between breeding seasons in calendar date from start of post guard. Two years of data are compared on a standardised time scale (see Figure 5.1). Data are presented in averages per week.

Within each breeding season, the difference in foraging trip duration between failed and successful breeders was not as marked as were the differences between breeding seasons. In 1995/96, successful breeders made longer foraging trips over time only in week 9 ($t_{35} = 2.26$, p = 0.030). In the 1996/97 season, successful breeders made significantly shorter trips than failed breeders only in weeks 5 and 6 ($t_{49.5} = 3.58$, p < 0.001 and $t_{54.4} = 2.13$, p = 0.038, respectively).

In analysis related to the age of the chick, foraging trip durations increased as chicks aged, in both breeding seasons. Breeders travelled between one to two days on average when their chicks were 1 to 5 weeks old, increasing to two to three day trips from when chicks were 6 weeks old until they fledged. Similar to the analysis over time, the patterns of trip duration against chick age were different between breeding seasons and between successful and failed breeders. Breeders in the 1995/96 season made longer trips on average than breeders in the 1996/97 season (Figure 5.9).

Analysing the group of successful breeders, birds made longer trips in 1995/96 than did birds in 1996/97. Trip duration exceeded two days when chicks were just 2 to 3 weeks

old in 1995/96 while two day trip duration was not exceeded in 1996/97 (ANOVA, $F_{9, 1952}$ = 2.22, p = 0.019).

Within each season, the difference in foraging trip duration between failed and successful breeders was not as marked as it was between breeding seasons. In the 1995/96 season, successful parents foraged significantly less time only when their chicks were 7 and 9 weeks old (t_{84} = 2.15, p = 0.035 and t_{35} = 2.26, p = 0.030, respectively) when compared with failed breeders which had chicks at the same age. In the 1996/97 season, successful parents foraged significantly less time when their chicks were 3 weeks old ($t_{63.5}$ = 2.88, p = 0.005), 4 weeks old ($t_{54.1}$ = 3.84, p < 0.001) and 6 weeks old(t_{15} = 2.72, p = 0.016) than did failed breeders which had chicks at the same age.
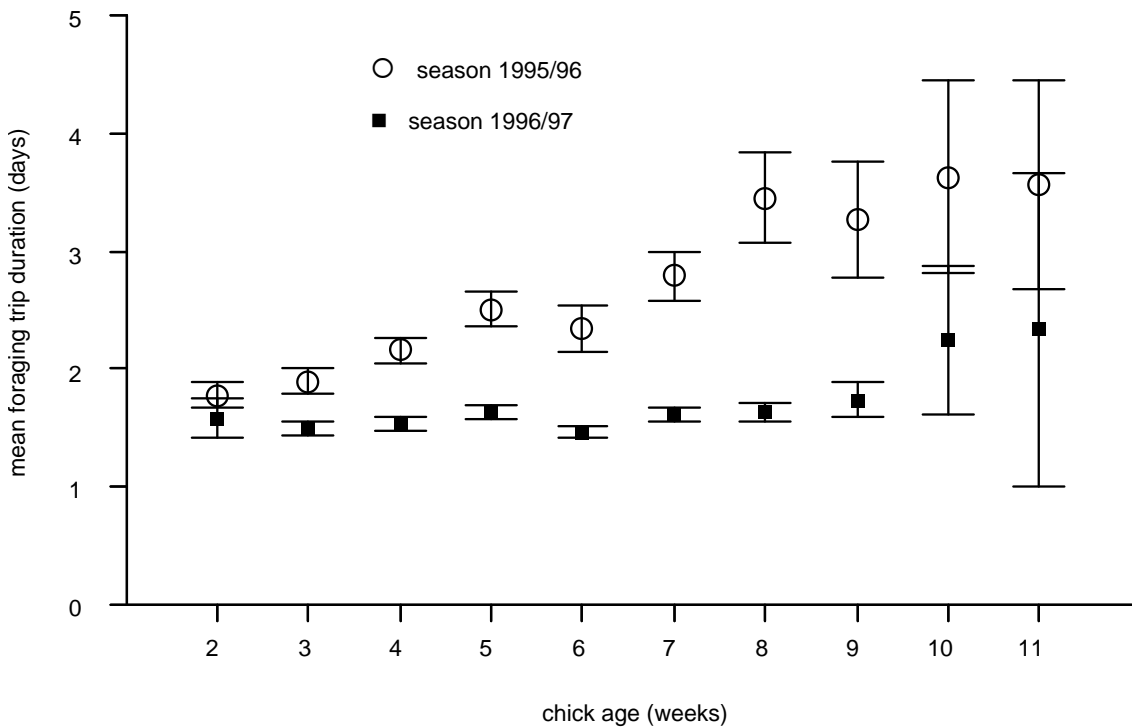
Figure 5.9 **The duration of foraging trips performed by little penguin related to the age of the chicks they were raising throughout two post guard periods. The durations of the trips were averaged over a week.**

5.3.6 *Total mass required*

It was calculated that to attain fledging condition each little penguin chick needed to be supplied at post guard with 13.8 kg of prey (Table 5.1). Based on results presented by Gales and Green (1990), in which penguin energetics was assessed using isotope

turnovers, a comparable prediction of chick requirements can be calculated. Assuming breeding little penguins consume 22kg more food than do non-breeding little penguins, and that ~ 55% of this is consumed during post guard chick rearing (Gales and Green 1990), approximately 12.6 kg of food would be available, above self-maintenance requirements, for provisioning of the chick. This food provisioning was likely to be based on fish since they comprised the main component in the chick diet (see Chapter 6).

In the1995/96 season, parents delivered between 170 and 200 tonnes of food to their chicks while in the 1996/97 season these values doubled. In an average season, chicks would require from 220 to 260 tonnes of food.

Season	Total consumption per fledging chick, kg	Total consumption per failed chick, kg	Number of chicks fledged per pair	Estimated consumption for all Phillip Is chicks, tonnes (1)	Commercial catch in PPb and Westernport Bay, tonnes (2)	Commercial catch in Victoria, tonnes (2)
1	14.6	6.4	0.3	175 - 205	1560	3324
2	13.1	8.0	1.3	358 - 418	1125	1824
Mean	13.8	7.2	0.8 (3)	228 - 265	2113	3744

Table 5.1   **Total food consumed per chick during the two breeding seasons, 1995/96 and 1996/97, at Phillip Island. The estimated consumption of all Phillip Is chicks (1) is based on a population between 12000 and 14000 breeding pairs (Dann, pers. comm.). Commercial catch (2) is based on contemporaneous data for Victoria (MFRI 1997). Mean values were calculated using meal mass from this study for total chick consumption per year, number of chicks per pair (3) from 20 years average for Phillip Island (Dann 1992) and commercial catch (2) from 5 years average, 1992 to 1997 (MFRI 1997). Commercial species were compiled according to the penguins' diet composition (see Chapter 6). PPB = Port Phillip Bay.**

5.3.7 *Sea surface temperature in the Bass Strait*

Sea surface temperature (SST) in Bass Strait varies throughout the year with different ranges in winter (10˚C-16˚C), spring (14˚C-18˚C), summer (18˚C-22˚C+) and autumn (14˚C-16˚C). For the period 1990/97, sea temperature reached 20˚C or more at the end of December except in 1997 when 20˚C occurred only at the end of January and also in the summer of 1995/96 when the temperature in Bass Strait did not cross the 20˚C band. The increase in temperature in summer is probably associated with the East Australian

Current (EAC) which moves southwards between December and January (see Figure 2.2). These warm waters (20˚C+) stayed for a period of 4 to 6 months. About a month after the EAC receded northwards, the SST at Bass Strait dropped below 16˚C reaching 10˚C-12˚C in mid winter. The time for this drop in temperature seems to be related to the force and length of time that EAC is present west of Bass Strait. Weak presence of the EAC resulted in earlier movement northwards.

5.4   Discussion

This chapter examines how breeding birds respond to fluctuations in food supply within breeding seasons and how the response differs between breeding seasons when breeding success is not similar.

5.4.1   Length of the chick rearing period and chick growth

During the chick guard period, all parents alternate daily between guarding the chick and foraging at sea, regardless of whether or not they are eventually successful at fledging the chick (Chiaradia and Kerry in press). In the productive 1996/97 breeding season, however, the length of guard period was 5 to 6 days longer and post guard was 9 days shorter than in the poor season. Longer parental care at guard suggests that parents in a good season provided more food at early growing stage of the chicks and therefore chicks grew faster and heavier than others from a shorter guard period in a poor season.

The little penguin chicks exhibited a decline in body mass prior to fledging like other penguin species, eg Adélie *Pygoscelis adeliae*, chinstrap *Pygoscelis antarctica* and *Eudyptes* penguins (Williams 1995). A drop in weight at the end of growth was different from that reported for little penguins by Gales (1987a) who showed that body mass continued to increase up to fledging. This different result may have been an artefact of sampling. In the present study, only chicks that fledged between ages 8 and 11 weeks were lighter than their peak values. Gales only reported the growth of chicks up to 8 weeks of age which probably does not relate to the whole age range of little penguin chicks. Considering that each species has a characteristic and inherent growth pattern (Ricklefs 1967), a decline in body mass prior to fledging probably better represents the chick growth of little penguins.

Stahel and Gales (1987) suggested that little penguin parents desert their chicks when they are close to fledging. Most fledging chicks in this study received a meal in the

night of fledging indicating that they had not been deserted. The decrease in body mass before fledging does not indicate that chicks are abandoned prior to fledging but that less food is delivered to them.

Cairns (1987) speculated that the growth rate of young chicks, whose food needs were small, tended to vary little between years of different food availability. In the present study, however, the growth rates of small chicks (~ 2 to 3 weeks old) were significantly different in consecutive years. This finding was in agreement with those of previous researchers who have suggested that chick growth is sensitive to variations in food supply as chicks grow more slowly and attain lower peak weights in years of lack of food compared with years of high food supply (Boersma 1978; Barrett et al. 1987; CCAMLR 1991). The growth curve in this study had a similar shape between breeding seasons but chicks from the good season grew faster and attained higher masses than chicks from the poor season. This suggests that the growth rates of little penguins might reflect food availability between breeding seasons.

5.4.2 Chick provisioning rates

Chick provisioning rates were analysed in relation to chick age and over time to examine whether meal masses delivered to the chicks were set by demands of the growing chicks or by food supply. Although the meal masses delivered to the chicks in the good season were heavier than those delivered during the poor season, the fluctuation in meal masses delivered over time followed a similar pattern but with a lag phase of about 4 weeks in 1996/97. This implies that there was an underlying factor acting on meal mass delivered that was in addition to food availability. The factor could have been age of the chick.

If variations in meal mass delivered by the parents were purely in response to their chicks' demand, meal mass would have the same patterns of intra and inter seasonal variations according to the chick age (Cairns 1987; Williams and Croxall 1990). This could be tested by examining the masses delivered to chicks that fledged. The successful breeders may be better than average foragers and able to negate the effects of inter-seasonal fluctuations in food availability. In contrast, previous studies have found evidence that seabirds are unable to respond to changes in nestling needs (eg Andersen et al. 1995). Dann (1987), however, showed that breeding success and chick mass at fledging did not change when the clutch was artificially enlarged which suggested that

parents increased the amounts of food brought ashore in response to an increased demand. This result could have been an artefact of an unusually good year of food abundance as was mentioned in the study. Dann's fledging chicks reached an average of 981g which was in excess of 100g more than the masses of fledged chicks in this study. The variation of chick body masses in this study had similar fluctuations to the meal masses. Chicks may need more food during their exponential growth from 1 to 6 weeks old which coincided with the highest average of meal masses delivered to them by their parents. After the age of 6 weeks, there was a decrease in meal mass delivered by the parents followed by a decrease in chick growth. The finding that chicks that fledged had similar changes in masses throughout both breeding seasons does suggest that parents adjust their provisioning rates according to age of their chicks.

5.4.3 Foraging trip duration

In this study foraging trip duration changed between years and over time within each breeding season. There appeared to be a threshold of two-day trips at post guard period; if birds kept their foraging trips below two days during the first 6 weeks of post guard their chicks survived, but if trips began to exceed two days, their chicks died. Thus, chicks younger than 5 weeks at post guard apparently cannot store more than two days worth of energy reserves. These reserves are potentially even less than this as I have only been considering the food supply from one parent. Chicks of other seabirds are capable of tolerating much longer periods without being fed (eg Bolton 1995; Hamer et al. 1998). The apparent lack of tolerance to starvation by little penguins may be related to their small size or their foraging strategies which may have evolved under more favourable conditions.

Weavers (1992) reported that little penguins make short (one day) and long ("several" days) trips. Collins et al. (1994) added that birds making long trips had chicks starving to death in the colony. This study showed that short trips are important in the first half of the season in contrast to the findings of Collins et al. Longer trips at the end of season do not indicate necessarily a failed parent as suggested by Collins et al. Foraging trip duration tended to increase towards the end of the season in both breeding seasons. These results suggest that the length of foraging trips may be driven primarily by food availability, as theorised by Cairns (1987), and not as a direct response to individual performance.

5.4.4 Foraging trip, meal mass and oceanographic conditions

Over the first 6 weeks of post guard in 1995/96, trip duration increased and meal mass decreased. After the sixth week, trip duration continued to increase while meal mass declined. In 1996/97, trip duration remained steady, at less than 2 day trips, until week 9 while meal mass remained steady until week 5 then declined. This fluctuation may be associated with the oceanographic conditions in the foraging zone of little penguins since there is evidence that sea surface temperature in Bass Strait influences little penguin breeding success at Phillip Island, perhaps by altering prey availability (Mickelson et al. 1992).

Comparing the sea surface temperature (SST) at west Bass Strait with fluctuations in the foraging trip duration and the meal mass brought ashore by little penguins, showed that birds tended to travel longer and meal mass delivered to the chick became lighter when the sea surface temperature was greater than 20˚C. The presence of the Eastern Australian current seems to increase the SST to above 20˚C in Bass Strait (Cresswell 1997 and Figure 2.2). The long term trend was more difficult to detect since the penguin data in this study corresponded to only two breeding seasons. There is evidence, however, that monthly and annual SST variations across Bass Strait explains 47% of the breeding success of little penguins on Phillip Island (Mickelson et al. 1992). A possible explanation for such events is a constant westerly wind bringing colder waters into the strait and, as a consequence, more nutrients (Gibbs 1992). Some little penguin's prey, like Barracouta *Thyrsites atun* and Pilchard *Sardinops sagax*, occur in waters between 9˚C and 21˚C (Kailola et al. 1993). An increase in temperature above 20˚C may push prey away from Bass Strait and cause birds to travel longer, use more energy and therefore bring less food ashore to their chicks.

5.4.5 Total mass required

Little penguins delivered to their chicks the equivalent of 13% to 37% of the total commercial catch landed in Port Phillip Bay and Westernport Bay, the two fishery landing ports around Phillip Island or between 6% to 23% of the commercial production for Victoria (MFRI 1997). If pilchard *Sardinops sagax*, which disappeared from the little penguin diet recently (see Chapter 6), is excluded from this analysis, the total food delivered to the chicks at Phillip Island would increase to 19% to 40% of the commercial fish taken in Victoria. These values are for the chick requirements only.

Little penguins may consume the equivalent of ~95% of the total commercial fish catch of Victoria per year, if the total energy used by the parents is considered using Gales and Green's (1990) energy budget. This calculation takes into account only the Phillip Island population where there is an accurate count of the size of the breeding population (Dann, pers. comm). The total catch by penguins would be substantial more if all little penguins from Victoria, including non-breeding birds were included.

As fish stock biomass is unknown for most of the commercial fisheries in Victorian waters (Kailola et al. 1993) one can not claim to have directly proved that there is competition between fisheries and penguins. However, the fact that penguins consumed almost the same order of magnitude of fish as was being caught by commercial fisheries suggests that penguins may influence the recruitment rates. Fisheries catch data are required for stock assessments and fisheries management but generally they are not sufficiently sensitive to provide a timely warning of fluctuations in recruitment (Butterworth in Crawford et al. 1983; Neira et al. 1997). Potential recruits appear in penguin stomachs several months before the fish grow large enough to be sampled in fisheries landing (Adams et al. 1992). Seabirds respond to decreases in stock and may help in understanding aspects of the ecology of fish stocks (Furness and Barrett 1991b; Shelton 1992). The little penguin has a limited foraging range at breeding and the waters adjacent to the colony are critically important to penguins' breeding success. The future of a sustainable food supply for the penguins may require a recommendation to control the fisheries in times critical to the little penguins to prevent overfishing in these areas.

6 The diet of little penguin Eudyptula minor at Phillip Island following the 1995 mass mortality of one of their main prey, the pilchard Sardinops sagax[6]

6.1 Introduction

At Phillip Island during the 1980s, little penguins *Eudyptula minor* preyed on a range of marine species, but two species were of primary importance; the pilchard *Sardinops sagax* and the anchovy *Engraulis australis* (Montague and Cullen 1988; Cullen et al. 1992). These two species regularly comprised more than 50% of the penguins' diet and apparently influenced the timing of breeding and breeding success of the penguins (Cullen et al. 1992; Hobday 1992). An abundance of pilchard and anchovy in the penguins' diet in spring appears to trigger the onset of early breeding, and the prevalence of these fish in the diet throughout the breeding period coincided with a better than average breeding success. In 1995, there was a mass mortality of pilchards in waters throughout southern Australia (Griffin et al. 1997). This mortality provided the opportunity to examine the changes in diet of little penguins in the event of possible depletion of pilchard in their foraging range. The present study was initiated to determine if the penguins were finding pilchards, and if not, what other prey were being targeted in the pilchards' absence.

Prior studies have demonstrated that little penguin diet varies between locations and seasonally at the same location (Klomp and Wooller 1988; Montague and Cullen 1988; Gales and Pemberton 1990; Cullen et al. 1992). This ability to vary their diet has led to the speculation that little penguins are opportunistic or generalist foragers (Cullen et al. 1992). Other penguin species, however, are thought to vary their diet depending on the requirements of their chicks (gentoo penguins *Pygoscelis papua*, Hindell 1989 ; Adélie penguins *Pygoscelis adeliae*, Kerry et al. 1997) which indicates a degree of prey selection is occurring. In several bird species the rate of food provisioning is regulated

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[6] Chiaradia, A., Costalunga, A. and Kerry, K. (2003). The diet of little penguins *Eudyptula minor* at Phillip Island, Victoria, following the 1995 mass mortality of one of their main prey, the pilchard Sardinops sagax. Emu 103: 43 - 48.

Chiaradia, A., Dann, P., Cullen, J. M. & Renwick, L. (2001). Effect of pilchard mortalities on the diet of Little penguins. New Zealand Journal of Zoology 28: 438 – 439.

by the interaction on energetic need of the chicks and parental response (Hussel 1991). The possibility that little penguins also can select prey to suit the requirements of their chicks has not been investigated previously. I examined prey selectivity in the little penguins by determining the diets of adults that were feeding known age chicks, and comparing changes in diet of the growing chicks with changes in their diet over time. This study was possible because the little penguins exhibit a prolonged egg laying period (6 weeks or more) which results in chicks of varying ages being present concurrently in the colony.

In summary, this study examines the diet of little penguins at Phillip Island, following a possible collapse in stocks of their primary prey, and investigates whether little penguins select prey according to the requirements of their chicks.

6.2   Method

6.2.1   Study site

The study site was about 800 m west of the Parade Colony at Sponge Cove (see Figure 2.1 in Chapter 2). The study site consists of natural burrows located along cliffs. About 150 burrows were marked individually and visited once a fortnight throughout two breeding seasons, 1995/96 and 1996/97. Birds were banded, weighed and sexed by bill measurements (P. Dann, pers. comm.). During each breeding season, the dietary sampling started within 5 days of the first chick's hatching.

6.2.2   Sampling of stomach contents

Food samples were collected by stomach flushing according to the method of Wilson (1984) modified by Gales (1987b). Birds were trapped using fences as soon as they arrived on the beach. Those eligible to be sampled based on their known breeding history were retained and all other penguins were released. Fences were removed when ten eligible birds were caught. Birds were then taken outside the colony and the flushing protocol started.

Under pressure, warm freshwater was pumped gently into each penguin's stomach through a plastic catheter, until water flowed back from its mouth. The catheter was removed, the bird was inverted over a bucket and pressure was applied to the base of the stomach using the thumb to push the food lump while the bird's beak was held open. Massage on the throat was undertaken to avoid any food blocking the passage.

In the first samplings, two birds died possibly due to hypovolemic shock caused by hyperthermia. To reduce the possibility of further casualties, some procedures were adopted. The number of flushings was limited to two for each bird and not three to ten used by Gales (1987b). About 40 ml of Vy-Trate®, a saline solution diluted 1/10, was given to the birds straight after the flushing ended to replace body salts lost during the flushing. Birds were released after 30 minutes. During chick rearing, birds received about 100 ml of homogenized fish to enable them to provide a meal to their chicks. This fish mix was given after assuring that birds were completely recovered. Two birds were observed feeding their chicks with the fish mix.

Additional procedures taken to minimize the impact on the birds included:

- Birds were released only after it was sure they had recovered sufficiently to aggressively defend their personal space.

- Special care was taken with birds that had full stomachs to avoid perforation of the stomach which has occurred in other studies (Clarke and Kerry 1994).

- Each bird was sampled only once in a breeding season. This meant that the chick(s) missed a maximum of 2 feeds.

- No sampling was carried out during the incubation period. At this time breeding birds fast for 3.4 days (range 1 to 18 days, Chiaradia and Kerry in press) and removal of stomach contents could have prevented birds from sustaining this fast, thereby causing desertion of the nest.

The project was approved by the Phillip Island Penguin Reserve and Koala Conservation Centre Animal Experimentation Ethics Committee and had a scientific permit issued by the Department of Conservation and Natural Resources.

6.2.3 Number of stomachs and frequency of sampling

During the breeding season, 10 stomach content samples were collected every 15 days from birds with known recent breeding histories. This sampling regime was comparable with frequencies adopted in previous studies: 7 to 24 stomachs at intervals of 4 to 30 days (Montague 1985; Klomp and Wooller 1988; Gales and Pemberton 1990; Cullen et al. 1992). Initial problems with the sampling protocol forced the interruption of sampling in the first season and only three out of eight planned sampling sessions were carried out.

6.2.4 Sample storage

Samples were frozen at -28°C for later analysis. After sorting, otoliths were stored dry and cephalopod beaks and small items such as crustaceans were preserved in solution of 70% alcohol containing 10% glycerin.

6.2.5 Identification and measurement of the prey

Otoliths and mandibles (for barracouta *Thyrsites atun* only) were used to identify the fish remains. The identification was carried out using reference collections of otoliths and otolith photographs that were supplied by Mike Cullen and Rosemary Gales. For fish in good condition, standard length (snout to tail base) was taken. Mantle length of cephalopods was measured for individuals in good condition. Most cephalopod beaks were removed from intact buccal masses but cephalopod mantles were heavily digested and only a few intact ones could be measured.

6.2.6 Analysis of stomach contents

Samples were drained, blotted dry and weighed to the nearest 0.1 g. The frequency of occurrence (FOO), weighted relative occurrence (WRO) and relative abundance were used to quantify the stomach contents.

FOO was the proportion of samples per sampling period that contained a particular taxon.

WRO represented the contribution by subjectively estimating the volume of each prey type relate to the total mass of food (Montague and Cullen 1988; Cullen et al. 1992). The categories for the subjective estimates were:

All	100%
Most	75%
Half	50%
Some	25%
Trace	10%
Insignificant	<1%

For a set of n samples, the WRO for each prey type was calculated as:

$$\frac{\sum_{i=1}^{n} (\text{volume category of prey type in sample i}) \times (\text{wet mass of sample i})}{\text{total wet mass of the samples}}$$

The WRO method prevents prey that are taken at low frequencies from being over represented in the analysis (see Cullen et al. 1992 for a detailed description). This

method was applied to compare the major prey categories of fish, cephalopods and crustaceans.

A third technique, relative abundance, was used to compare the occurrences of different fish species. The relative abundance of these fish was calculated by dividing the total number of sagitta otoliths from a sampling period by two, then calculating the proportional representation of each species. This method tended to inflate the importance of small prey (see Duffy and Jackson 1986) but WRO was used to exclude from the analysis those 'trace' prey which were numerically abundant but volumetrically irrelevant. It was assumed that the fish species were of similar size (Cullen et al. 1992) and relative abundance was therefore a suitable measure of diet (Duffy and Jackson 1986).

6.3 Results

A total of 89 stomach contents of little penguins was sampled; 11 from the first breeding season (Nov – Dec 1995), 9 from the period between breeding seasons (Mar – Jul 1996) and 69 from the second breeding season (Sep 96 to Feb 97).

6.3.1 Adult body mass and stomach content

Adult body mass of the penguins tended to increase during the early stages of the breeding season, reached a peak during the chick guard period, and then decreased as the chicks grew (Figure 6.1). Overall, males averaged significantly greater body mass than did females (male = 1277 ± 146g, n = 41 and female = 1162 ± 173g, n = 37, t_{76} = 3.15, p = 0.002).
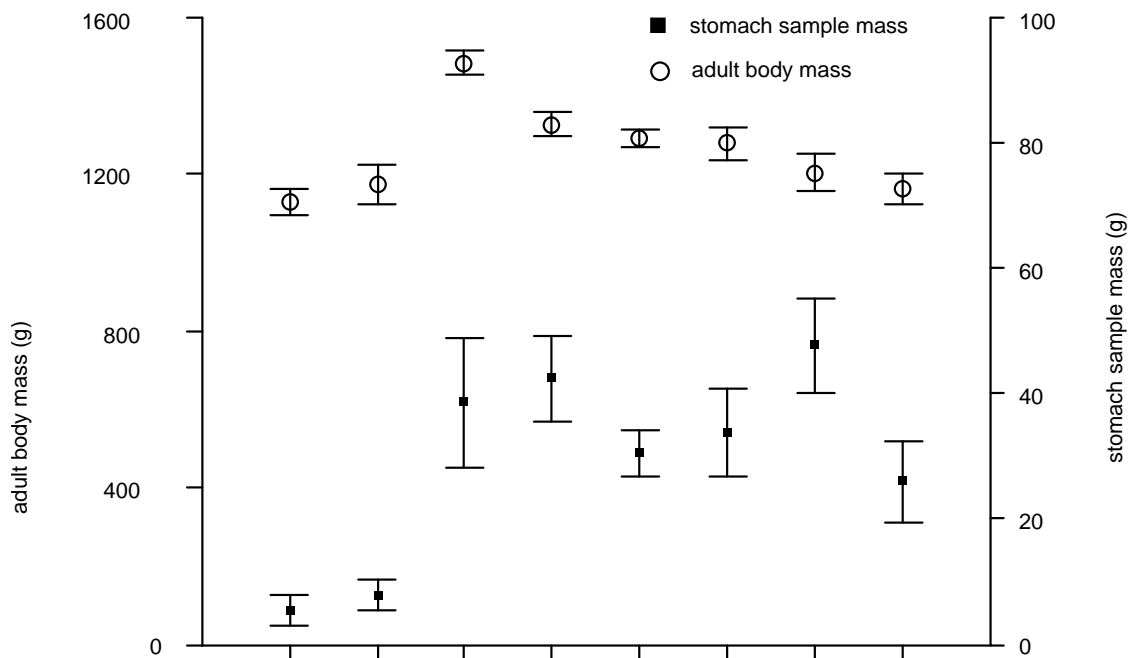
Figure 6.1 **Mass variation of little penguins and their stomach contents during sampling over the 1996/97 breeding season. Sample mass was subtracted from the adult mass in the plot. Mass ± SE is represent in two scales in each y axis.**

Four of the 89 stomachs flushed were empty and a further 15 contained less than 1 g of contents; typically they contained just prey hard parts such as cephalopod beaks, otoliths or a few crustaceans. Stomach contents were substantially heavier when birds were feeding chicks (36 ± 20.4g, n = 54) than they were at other times (4 ± 6.1g, n = 31). The mean sample mass tended to be smaller as the chicks grew (Figure 6.2).

During chick rearing, there was no significant difference between sexes in the mass of stomach contents brought ashore to feed the chicks ($t_{48} = 1.10$, p = 0.270). This result conflicts with the observation of Hodgson (1975) that male little penguins tended to bring larger meals to their chicks than did females.
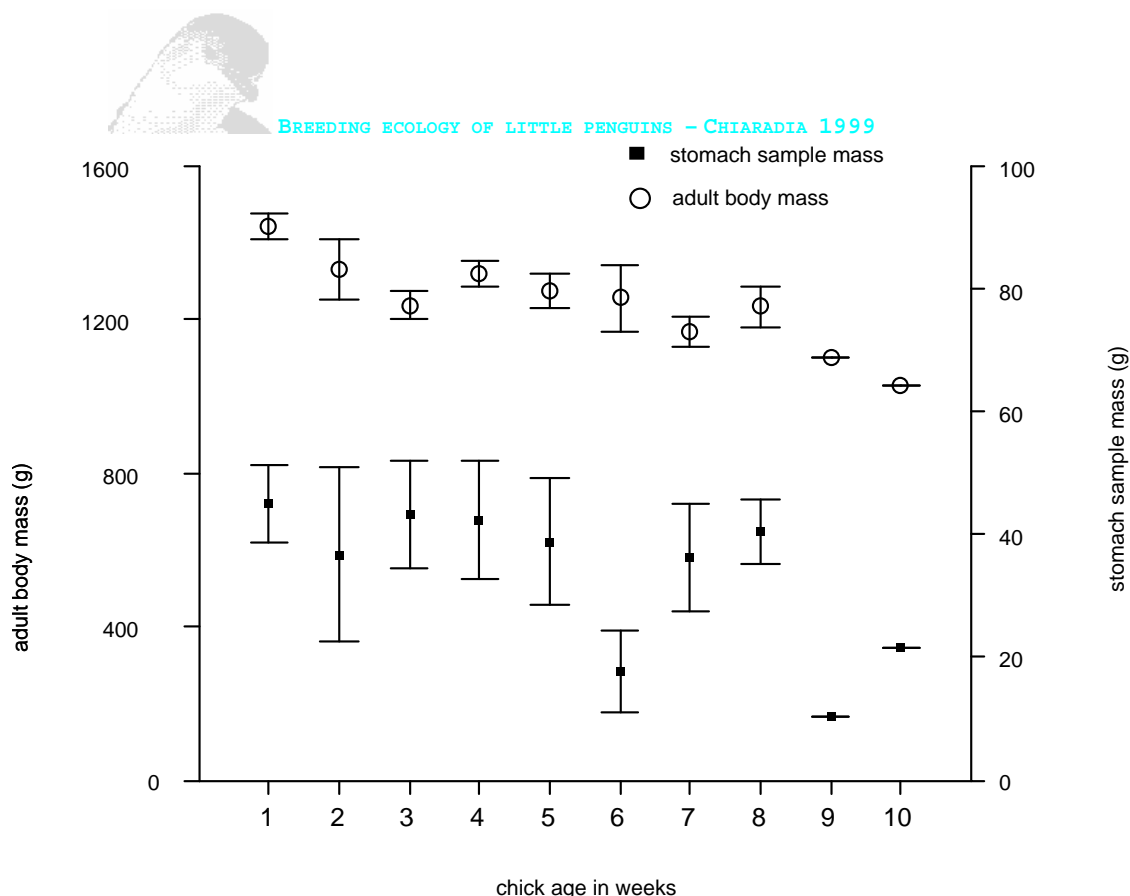
Figure 6.2   Mass variation of adults and their stomach contents relative to the age of their chicks. Mass ± SE is presented on two scales in each y axis.

6.3.2 Diet composition

Sixteen species of fish, five of cephalopods and four species of crustaceans were identified. Using frequency of occurrence, fish appeared on 74% of the samples followed by cephalopods (72%) and crustaceans (57%). The presence of cephalopods was inflated towards the end of breeding season using frequency of occurrence. The weighted relative occurrence (WRO) provided a more realistic representation of the diet composition (Figure 6.3). The frequency of occurrence of shells was 7%, seagrasses 6% and rocks 2%.

Based on the WRO estimated composition, the penguins' diet comprised 82% fish, 12% cephalopods and 3% crustaceans. These percentages were comparable to those reported by Cullen et al. (1992, 82%, 14% and 3% respectively). In March and July, the penguins were eating mainly cephalopods and crustaceans. The proportion of fish eaten was low at these times but increased in importance through the year and dominated the diet between October and February (egg laying until chicks fledged, Figure 6.3). This was a similar pattern to that observed previously for the same site and in Tasmania (Gales and Pemberton 1990; Cullen et al. 1992).
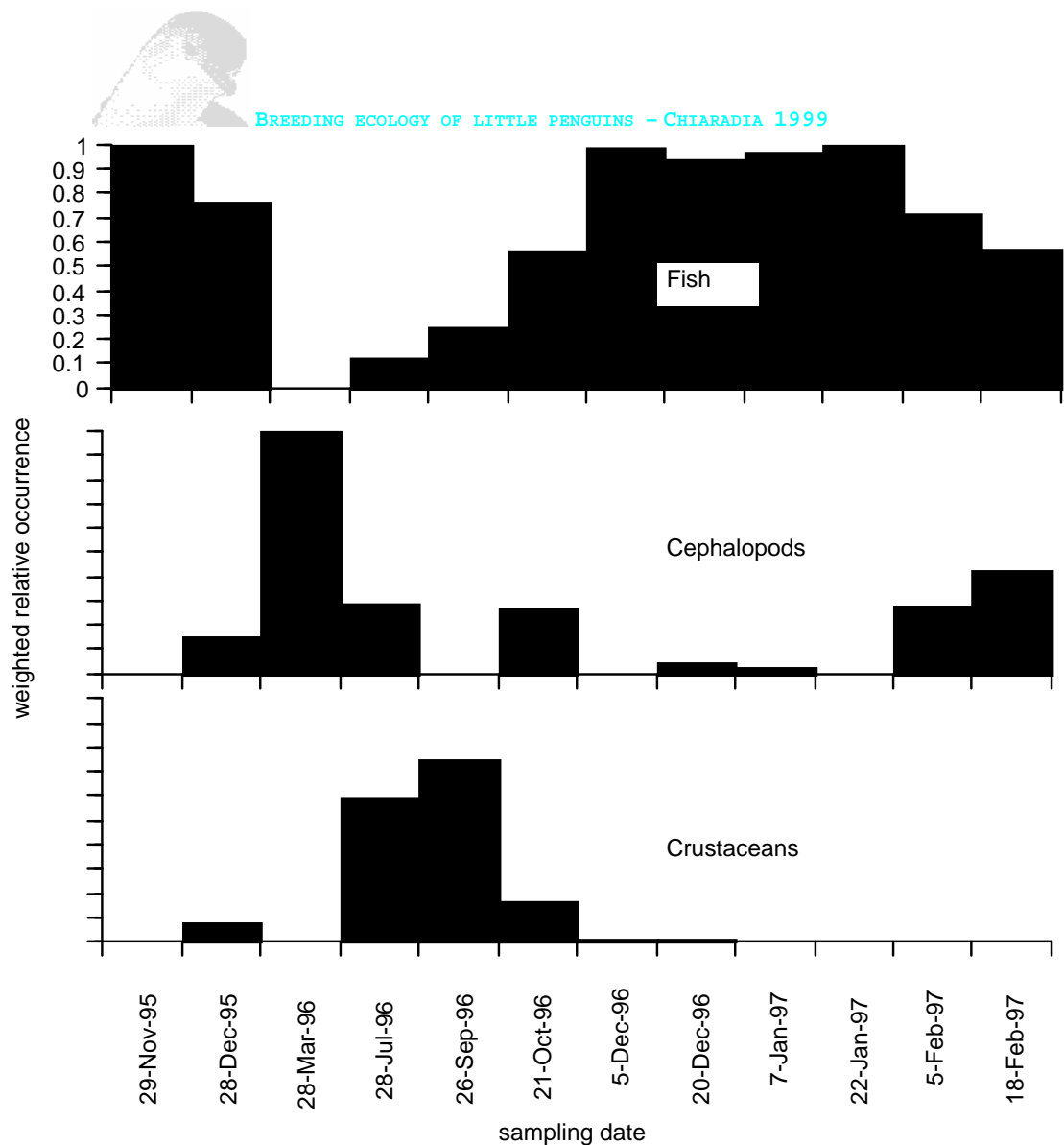
Figure 6.3 **Proportion of the three main prey groups in the penguin's diet at sampling date over two breeding seasons, 1995/96 and 1996/97. The proportions are based on the WRO method.**

6.3.3 Fish

Fish appeared in the diet of the penguins on every sampling occasion except in Mar 96, when only cephalopods were present (Figure 6.3). Pilchard *Sardinops sagax* was present in the penguins' stomachs only as a trace in this study (FOO 4%).

WRO could not be applied to individual fish taxa since most of the stomach contents were digested. For post-larvae, leatherjacket *Tetraodontiformes*, and seahorses *Hippocampus* sp. which occurred in near-intact condition, WRO percentages of less than 4% were recorded. Comparisons of the proportions of other fish in the penguin's diet, based on the relative abundance of their otoliths, indicated species were taken sequentially over time (Figure 6.4).
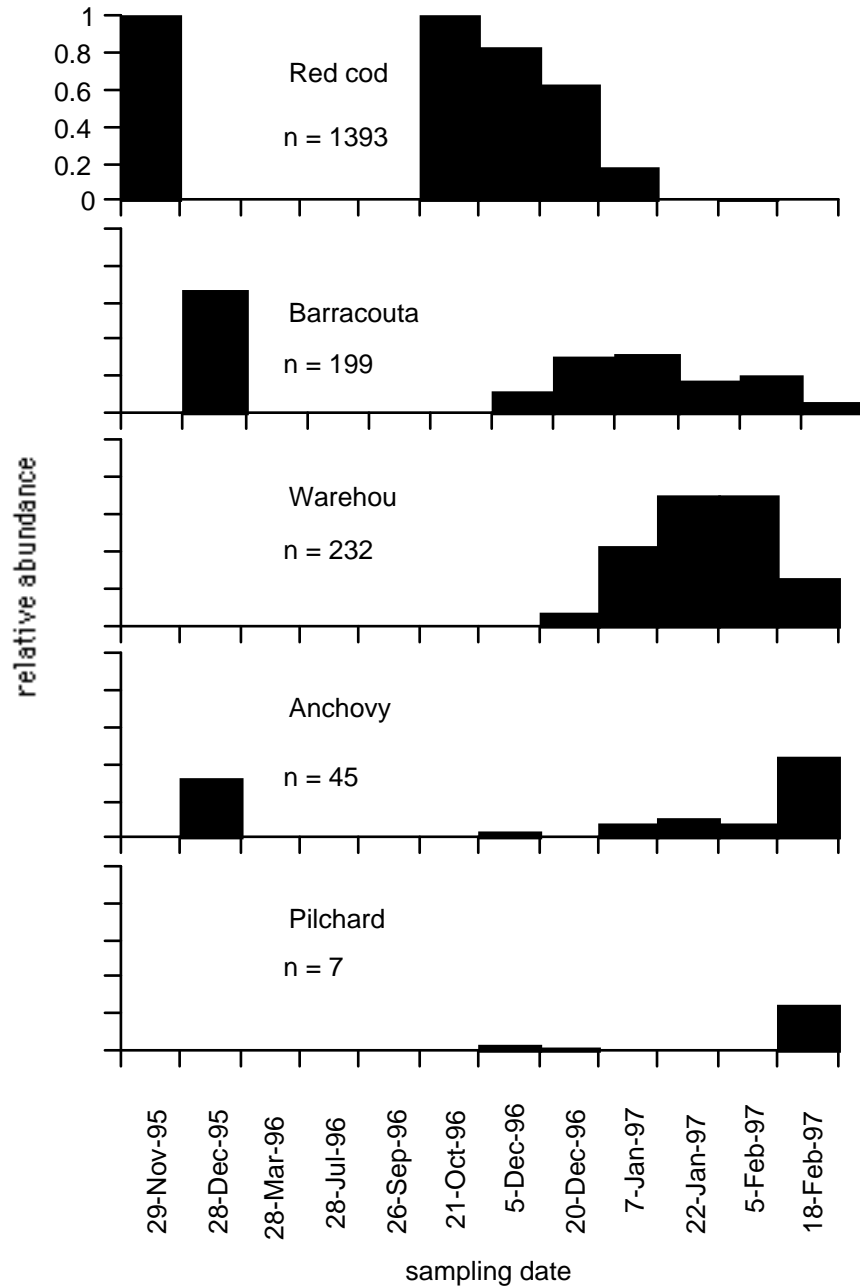
Figure 6.4 **Seasonal succession of the main fish prey in the penguins' diet represented by proportion of relative abundance at sampling date over two breeding seasons, 1995/96 and 1996/97. n = total number of individuals of each species. Pilchard was included for comparison (see text).**

Red cod *Pseudophycis bachus*, barracouta *Thyrsites atun*, warehou *Seriolella brama* and anchovy *Engraulis australis* represented 93% of total relative abundance of fish prey species. They were assumed to be more or less of the same size and therefore suitable to be represented by relative abundances (Duffy and Jackson 1986; Cullen et al. 1992).

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Overall, red cod had the highest relative abundance in the penguins' diet followed by barracouta, warehou and anchovy. In October, when most penguins were mating or sharing incubation shifts, red cod were the main prey. Penguins continued to consume more red cod than any other prey species during November and December. In late December/ early January, however, firstly barracouta, then warehou became more frequently preyed upon than the red cod. This trend was apparent in both breeding seasons, 1995/96 and 1996/97 (Figure 6.4).

Penguins consumed much less anchovies than the red cods, barracoutas and warehous except in the last sampling session when anchovies reached a relative abundance of about 30% (Figure 6.4). Only trace amounts of pilchards were recorded throughout the season except for a relative abundance of 25% in the last sampling session (Figure 6.4). In the last sampling session, however, penguins were preying on as much fish as cephalopods and the stomach content mass was on average half of the previous sampling sessions.

6.3.4 Cephalopods

The main cephalopods taken by little penguins were Gould's squid *Nototodarus gouldi* (FOO 66%) followed by squid *Loliolus noctiluca* (FOO 10%), southern calamari *Sepioteuthis australis* (FOO 9%) and octopus *Argonauta nodosa* (FOO 9%). A small octopod, identified to the order level only and probably a post-larvae, was present in 11% of samples.

Gould's squid was always the main prey when cephalopods comprised more than 10% of WRO (Figure 6.3). In the last two sampling sessions Gould's squid had a WRO of 27% and 42%; some birds had 100% of Gould's squid in their stomachs. In these two sampling days Gould's squid mantles ranged from 19 to 82 mm (mean = 37 ± 11.2mm, n = 59). This high presence of squid in the stomachs coincided with a presence of several squid fishing boats close to the island on the night of sampling.

6.3.5 Crustaceans

Krill *Nyctiphanes australis* (FOO 43%) was the crustacean most frequently consumed, followed by amphipods (FOO 22%), brachyurans (FOO 16%) and stomatopods (FOO 11%). Very few individual amphipods (median = 2, range 1 - 7) and brachyurans (median = 1, range 1 - 32) were found in the stomachs and they had no substantial volume at any time. Krill (median = 5, range 1 – 1256) and stomatopods (median = 13,

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range 1 – 158) were important components of the adults' diet prior to breeding but they did not contribute substantially to the volume of food delivered to the chicks (Figure 6.3).

6.3.6 Diet in relation to the age of the chick

The diet composition of little penguin chicks was examined by sampling adults which had chicks of known ages (n = 54 birds). Little penguin chicks fledge between 7 to 11 weeks (median = 9 ± 1.1 weeks, n = 114; see Chapter 5) and an attempt was made to sample birds with chicks of all ages. Fish constituted 80% to 100% of the diet of 0 to 5 week old chicks (Figure 6.5). At 6 weeks of age, chicks were fed a mixed diet of 50% fish and 50% cephalopod. After the sixth week, fish again dominated the chicks' diet and steadily increased to 80% of the diet of 8 to 10 week old chicks.
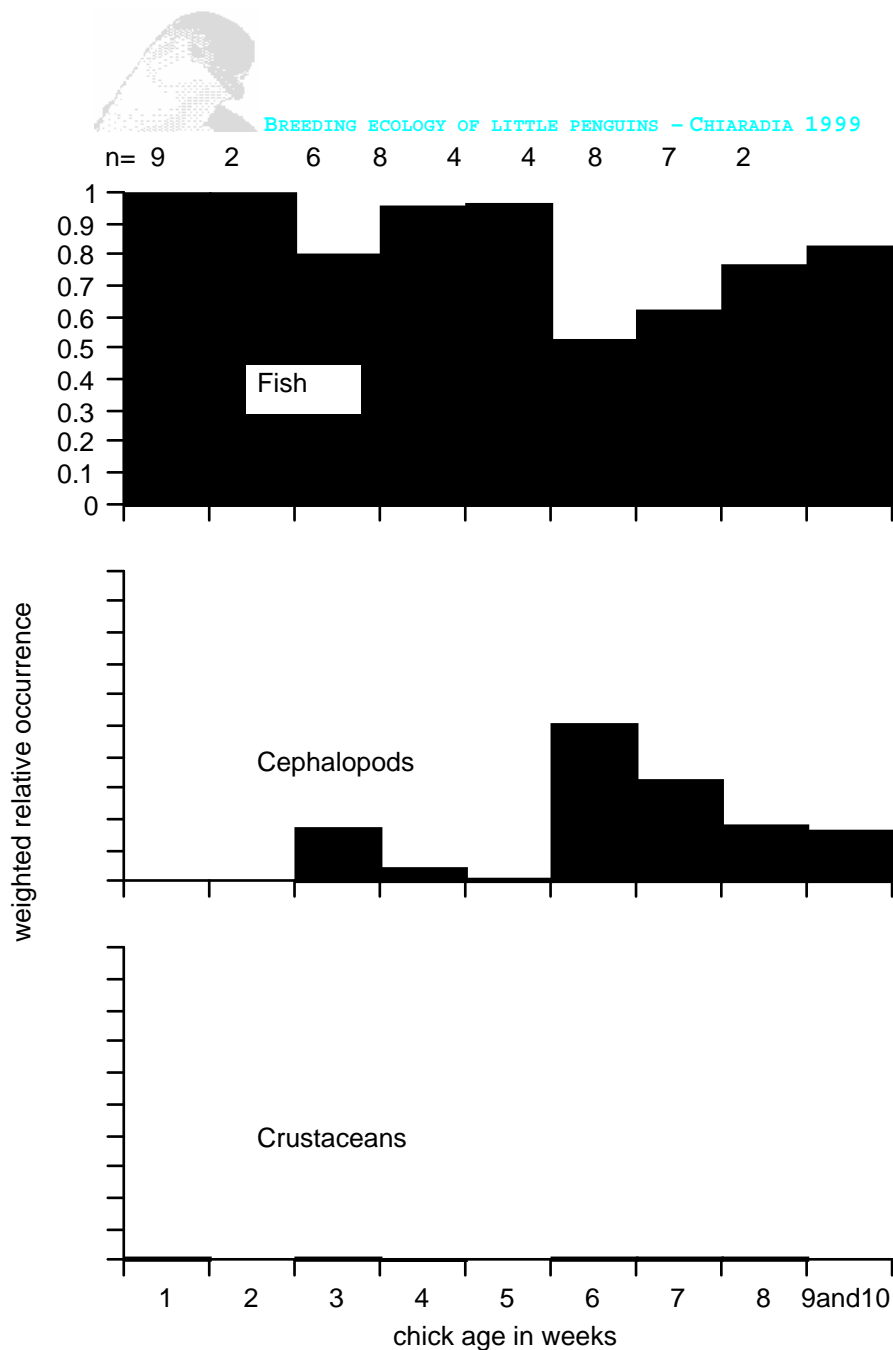
Figure 6.5 Proportion of the main prey groups in the diet of little penguin breeders relate to their chicks' age. The proportions are based on the WRO method. The sample size is represented at the top and ages 9 and 10 were combined for the analysis due to the small sample size.

A similar succession of fish observed overtime was also observed in the diet according to the chick age. Although red cod was the most abundant fish overall (Figure 6.4) it contributed substantially only in the diet of one week old chicks (Figure 6.6). Warehou followed by barracouta were the main fish prey for the chicks of all ages. Anchovy was the major component in stomach contents of one parent that had a 9 week old chick. Apart from this occurrence, anchovies were not abundant in the stomachs (Figure 6.6).

Pilchard appeared only as a trace component in some samples. Chicks aged 9 and 10 weeks had only one parent sampled each time and these results may be a poor representation of the diet for these stages.
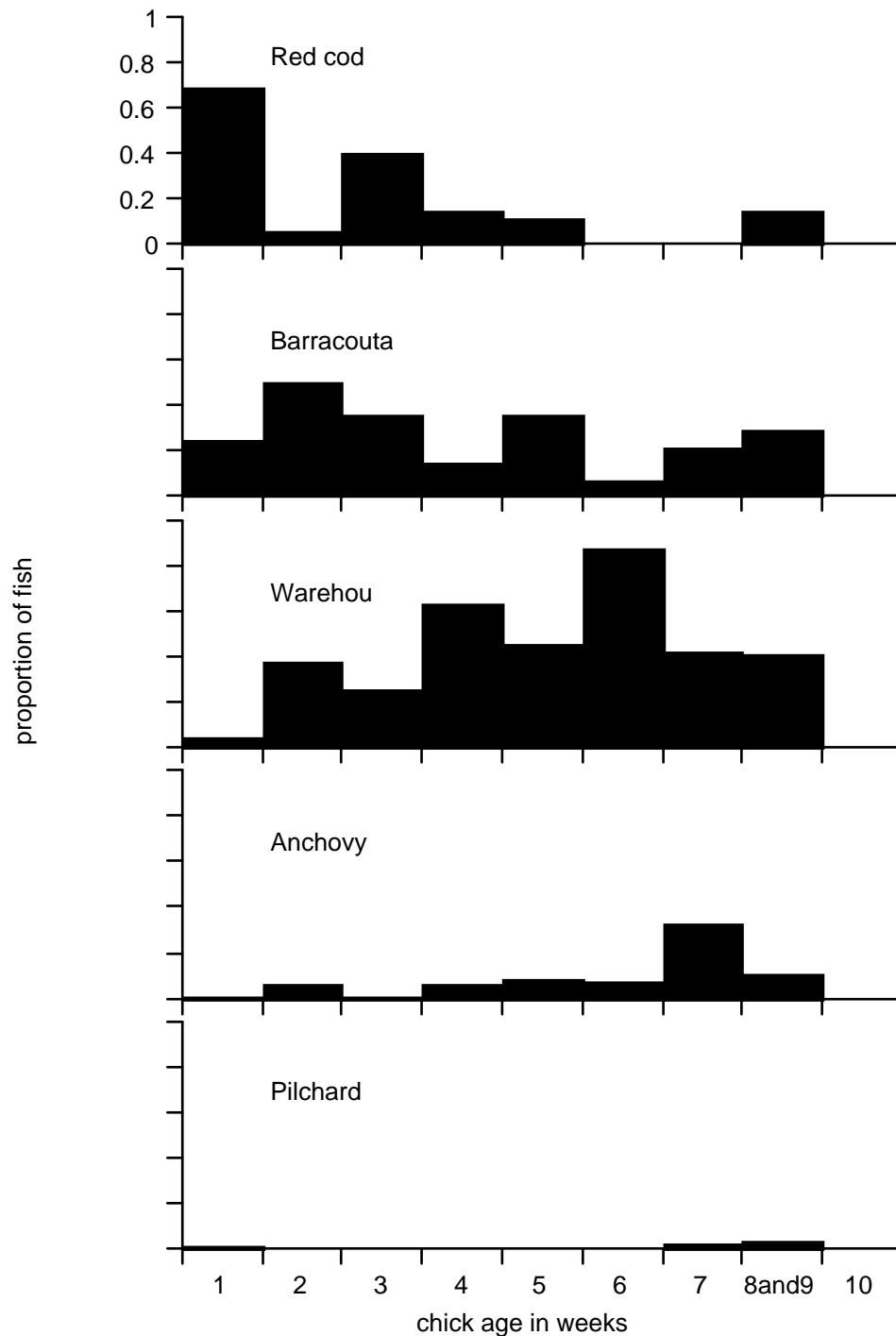
Figure 6.6   Changes in the proportions of selected fish species that adult little penguins fed to their chicks, as the chicks grew during 1996/97. The proportions are based on the relative abundance of otoliths from the fish. Note that chick ages 8 to 10 were combined because of small sample size.

Changes in the stomach contents of parents feeding known age chicks of 1 to 7 weeks of age (too few from those feeding older chicks) were compared with the temporal changes. The diet of chicks as they grew (Figures 6.5 and 6.6) did not vary substantially from the apparent temporal changes in prey available to the parents (Figures 6.3 and 6.4) suggesting that the parents were opportunistic rather than selective feeders.

6.4 Discussion

The impact of a massive mortality of pilchard on the little penguin diet is examined in this chapter. Prey variability and availability and the relative importance of increasing chick demands are inferred by examining the diet of breeders with known breeding history. This study was conducted during two breeding seasons and discussion concentrates on the second season since only three out of twelve sampling sessions were made in the first season.

6.4.1 Diet composition

The diet composition of little penguins at Phillip Island was clearly different from their diet over the last decade (Table 6.1). Pilchard has virtually disappeared and anchovy decreased markedly in frequency of occurrence in the penguins' stomachs. They have been replaced by red cod, barracouta and warehou. The frequency of occurrence of Gould's squid has remained constant since the first diet study at Phillip Island (Montague and Cullen 1988; Cullen et al. 1992). Some of the increase in presence observed in less frequent species (10% or less, see Table 6.1) may be caused by biases in the method of frequency of occurrence which tends to inflate the importance of less frequent items and over-represent prey that remain longer in the stomachs (Pierce and Boyle 1991). Barracouta, red cod and warehou showed the greatest increase compared with the previous studies (Table 6.1) and they were the most abundant species during the breeding season. These fish were not present in the non-reproductive season and started to appear in the samples just before laying.

		1995-97 (1)	1985-88 (2)	1979-83 (3)
Fish	Barracouta	38	16	9
	Warehou	37	3	<5
	Red Cod	36	8	8
	Leatherjackets	30	18	11
	Post larvae-unidentified	22	-	-
	Anchovy	19	30	61
	Atherinason sp	13	<5	<5
	Hippocampus sp	10	7	1
	Sandy Sprat	10	<5	<5
	Red Mullet	6	-	-
	Pilchard	4	25	51
	Heteroclitus	1	-	-
	Gurnard	0	13	2
	Garfish	0	6	1
	Unknown fish	12	-	-
Cephalopods	Gould's squid	64	70	25
	Octopodidae	11	<5	<5
	Loliolus	10	8	3
	Sepioteutis australis	9	2	-
	Argonauta nodosa	9	24	8
Crustaceans	Nyctiphanes australis	42	25	1
	Amphipoda	21	4	-
	Brachyura	16	5	1
	Stomatopoda	11	3	-

Table 6.1 **Comparison of frequency of occurrence in percentage of the prey items observed in the stomach contents in this study (1) and others carried out at different times at Phillip Island (2, Cullen et al. 1992 and 3, Montague and Cullen 1988). Main prey fish and pilchards are highlighted and (-) indicates absence of information.**

Barracouta, red cod and warehou spawn in Victorian waters in winter and spring (Kailola et al. 1993). Juveniles inhabit sheltered waters of bays and estuaries. They grow quickly reaching between 23 to 30 cm in the first year (Kailola et al. 1993). Little is known of the early development of these three species but the penguins were probably feeding on very young fish since little penguins prey on individuals smaller than 12 cm (Cullen et al. 1992). Anchovy spawn in inshore and bay waters and the juveniles stay there until maturity at two years old or more when they move into open waters in winter and return inshore in spring (Kailola et al. 1993). Pilchard spawn in continental shelf waters of Victoria, probably within 10 km of the coastline, during spring and summer (Hoedt et al. 1995). Post-larvae move to bays, inlets and estuaries and remain in this region for between 8 and 12 months. Pilchard and anchovy reach 6 to 8 cm in one year (Kailola et al. 1993) and therefore remain at a size capable of being

exploited by penguins for a much longer period than do red cod, barracouta and warehou.

6.4.2 Pilchard and anchovy disappearance

A massive mortality of adult pilchards from March to June1995 raised the question of how little penguins would cope with an absence of one of their principal prey (Hobday 1992). An effect upon the little penguin population from this mortality, when juvenile pilchards would not be consistently available to the penguins, would be expected after 18 months.

In the season following the pilchard mortality, two sampling sessions on November and December 1995 showed no trace of pilchards. Although pilchards are expected to be in the little penguins stomachs at this time of the year they were not present in some years as reported in summer 1987 which coincided with a poor breeding performance (Montague and Cullen 1988; Cullen et al. 1992). Later availability of pilchards and anchovies in the little penguin foraging range has been associated with a delayed onset of breeding and poor breeding performance of the penguins (Hobday 1992). In the season following the pilchard mortality, the breeding success averaged 0.3 chicks per pair which was one of the lowest breeding performances compared with a 20 year average of 0.8 chicks per pair with a production of 0.17 chicks per pair the lowest chick production ever recorded (Dann and Cullen 1990). Pilchard was absent in the penguins' stomach in this season but the sample size was too small to reach any conclusions on diet changes.

In the second breeding season (1996/97), after an interval of 18 months following the pilchard mortality, little penguin diet composition was dominated by red cod, barracouta, warehou and some anchovy. Pilchard was only in trace amounts in the sample. These results suggest that the pilchard mortality had an effect on the little penguins at Phillip Island, which resulted in a different diet composition compared with the last decade (Table 6.1). Their breeding performance, however, was above average (1.34 chicks per pair) in the second breeding season after the pilchard mortality which indicates that the penguins can breed successfully while preying upon other species.

The massive mortality of clupeoids in southern Australia apparently affected only adult pilchards (Griffin et al. 1997) so the decrease of anchovy in the penguins' diet was unexpected. Pilchards and anchovies school together and the availability of anchovies to

the penguins may be associated with the schooling behaviour of these two clupeoids (Hobday 1992). Contemporaneous aerial surveys of fish schools reported the presence of anchovy near to Phillip Island (Neira 1997). Anchovy was present in the foraging range of little penguins but probably in lower abundance than they used to be when schooling with pilchard and therefore not available to the penguins.

6.4.3 Commercial catch

Commercial catches of pilchard did not drop in the summer 1995/96 compared with catches in other years (MFRI 1997). In 1996/97 however, the pilchard catch dropped to 32% of the catch recorded in 1995/96 (2,346 to 773 tonnes). The initial stock size of pilchard was unknown, but Cox (1995) speculated that 10% of the population may have perished. The low landing reports and the disappearance of pilchard from the penguins' diet in this study, however, suggest a higher impact caused by the 1995 event.

On the other hand, in 1996/97, anchovy catches increased by 34% (645 to 868 tonnes) perhaps because fisheries switched to anchovy after the pilchard mortality (Figure 6.10). In the south east Atlantic, there was a similar occurrence with anchovy replacing pilchard in catch following a collapse of pilchard stocks off South Africa and Namibia (Shelton 1992). There is a possibility that the greater fisheries' pressure on anchovies reduced anchovy stocks that were available to Phillip Island little penguins and this caused the reduced presence of anchovies in the penguins' diet.

Fisheries competing with seabirds for local resources causing changes in the birds diet and breeding performance has been shown in other parts of the world. In the Shetland archipelago in the North Sea, Sandeels *Ammodytes marinus* virtually disappeared from the diet of some seabirds after the establishment of a Sandeel fishery in the area (Furness and Barrett 1991b). There, Sandeels were the main prey of more than one million birds (22 species) and their decline has affected those bird species that had limited foraging range or with specialised and inflexible feeding habits (Furness and Barrett 1991a). The marine system in Victorian waters is simpler than the North Sea; it sustains a modest fishery and has less diverse seabird population (Norman 1992; Kailola et al. 1993; Norman et al. 1996). Although commercial fisheries are concentrated in Port Phillip Bay and there is not direct overlap between fisheries and the foraging range of Phillip Island penguins, there is evidence that the Phillip Island region is a spawning area and contributes to the recruitment of pilchards and anchovies into

Port Phillip Bay (Kailola et al. 1993; Collins et al. 1994; Hoedt et al. 1995). Pilchards and anchovies declined in predominance in the penguin diet at the same time as commercial catches of these species were increasing progressively (Neira et al. 1995; 1997). Little penguins at Phillip Island harvest at the same order of magnitude in tonnes as the commercial fisheries (Chapter 5) which indicates a potential competition between fisheries and penguins. Changes in commercial catches may have affected the availability of penguins' prey. Little penguins have a versatile diet and they can switch to other prey and cope with prey availability as shown in this study. But penguins have a limited foraging range and a synchronised succession of red cod, barracouta and warehou may not happen every season. Reproductive levels will depend on how reliable is the availability of these prey species, also targeted commercially, in future breeding seasons and what are the alternatives when neither prey is available in synchrony.

The pilchard mortality of 1995 has been providing a natural experiment to test the effects of pilchard availability on the penguin breeding performance. The real size of anchovy and pilchard stocks in Victorian waters is unknown and there is no estimate of how much more the fishing industry can harvest but their stocks are considered to be not fully exploited (Kailola et al. 1993). Continued monitoring of the diet of little penguins at Phillip Island will provide information on future changes of pilchard stocks. At the same time, anchovy has dropped in abundance in the penguins' diet and further investigation could reveal whether this event has any link with the increased catch by the commercial fishery.
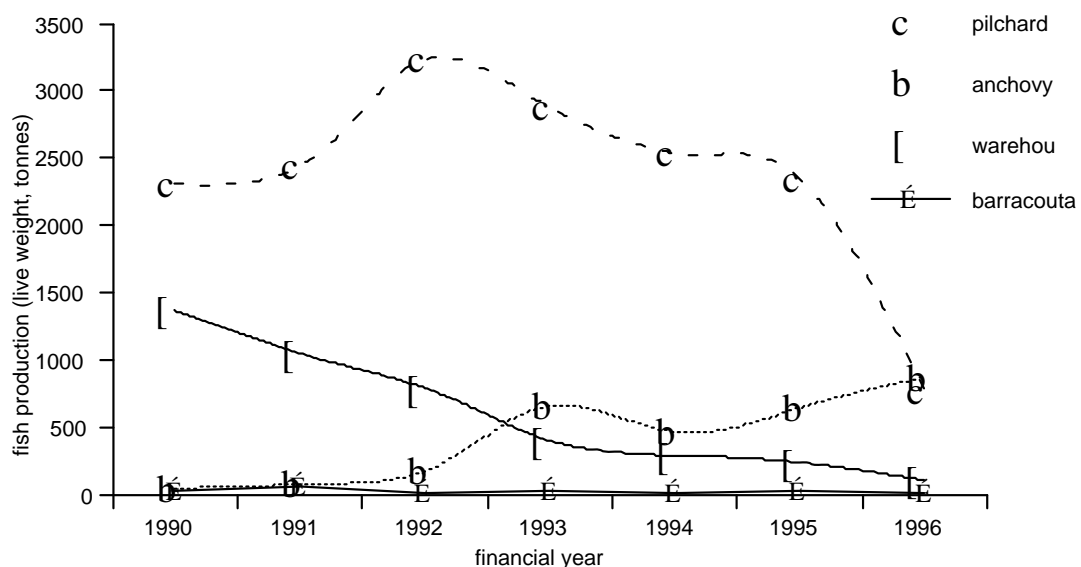
Figure 6.7 Commercial catches of four fish species, also common in the little penguin diet, in the last six financial years (July to June). There are no data available on red cod although it is caught commercially. Extracted from the information bulletin on catch and effort of Victorian fisheries (MFRI 1997).

6.4.4 Are little penguins partially selective foragers?

Seabirds are adapted to situations where the food availability rarely falls below the limit required to the survival of the adults (Cairns 1992b). The major task of the parents during the chick rearing period is then to provide food to their chicks in short and regular intervals of time. Seabirds, particularly penguins, feed in a limited foraging zone during breeding which can cause a food depletion near the colony as the season progresses (Ashmole 1971; Birt et al. 1987). Birds need to take advantage of the best time of the year to start to breed in order to provide high energy food at least during the first 6 weeks of the exponential growth of the chicks. They may prefer to feed on fish which have a higher energy content than cephalopods and krill (Gales and Pemberton 1990). All these factors impose temporal and geographic constrains on the seabird foraging behaviour and seabirds will respond differently to this limiting factor according to the availability of food (Barrett 1992; Cairns 1992b). In Chapter 5 it was suggested that the food provisioning to the chicks of little penguins is partially a response to the growing chick. However, the diet composition related to the age of the chick did not contrast from the temporal changes in prey available to the parents. This agrees with Cullen et al. (1992) that the diet composition of little penguins reflects food availability and they are probably opportunistic rather than selective feeders.

Temporal sampling and chick age were not totally independent events since sampling started as soon as the first group of eggs hatched and fewer later breeders were sampled; and therefore the results may be biased towards the early breeders. This was the first time that the diet composition of little penguin chicks was examined and it was restricted to one breeding season. Future inter-seasonal research on little penguin diet, using breeders with chicks of known age needs to address whether the non-selective feeding behaviour is responsive between breeding seasons of different food availability.

7   General conclusion[7]

This study records aspects of the breeding biology and feeding ecology of the little penguin *Eudyptula minor* throughout 1995/96 and 1996/97 breeding seasons. This study was initiated as a first step to assess the little penguin as an indicator in a monitoring program that examines changes in the availability of prey in the marine ecosystem around Phillip Island. The approach taken was similar to that for monitoring Adélie penguins as part of the CCAMLR[8] Ecosystem Monitoring Program (CEMP). Parameters related to the breeding biology and feeding ecology of the little penguin were selected based on the CEMP experience. These parameters were thought likely to reflect changes in the food supply available to the little penguins during the breeding period.

The 1995/96 breeding season was characterised by poor breeding success where only 0.3 chicks were fledged per breeding pair. This compares with a 20 year average of 0.8 chicks per pair (Dann and Cullen 1990). The 1996/97 breeding season by contrast had very good reproductive success producing 1.3 chicks per pair. The difference between these two seasons was attributed to availability of food within the normal foraging range of little penguins from Phillip Island. This attribution could only be inferred since it was not possible to obtain contemporaneous data on the distribution and abundance of prey items and only one full breeding season's data (1996/97) on diet composition was collected. However given the variation in measured variables between the two seasons, it is clear that the major differences were brought about by changes in food availability (Table 7.1).

The 1996/97 breeding season (good season) in contrast to the 1995/96 breeding season (poor season) was characterised by shorter duration of foraging trips and parents delivering a larger meal to their chicks. The period over which a parent remained with

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[7] Chiaradia, A. 2001. Using penguins to help to save the fish. Turning the Tide 2: 19.

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the chicks, the guard period, was longer but the period to raise a chick to its peak weight was one week shorter.

Differences for some variables during the course of each season were apparent as well. For instance, successful breeders undertook shorter incubation shifts, which equated to shorter foraging trips by the partner, and made more foraging trips than failed breeders. This was more pronounced in the bad season. The foraging trip duration was always shorter in successful breeders of both seasons. Chick growth was slower for all birds in a bad season.

This study involved two very different breeding seasons which have pointed to how variables related to breeding biology and feeding ecology respond to food supply (Table 7.1). This suggests that a monitoring program to provide detailed information for use in the conservation of the little penguin and its prey could be established by recording these and related variables each season for a number of years.
Although the little penguin is not threatened at present there is an unregulated fishery based upon several major prey items. These species are pilchard *Sardinops sagax*, anchovy *Engraulis australis*, red cod *Pseudophycis bachus*, barracouta *Thyrsites atun*, and warehou *Seriolella brama*. The overfishing of these species could compromise the penguins' food supply in the future.

The variables measured in a monitoring program must have a predictable response, be easy to measure and above all be sensitive to change in the availability and quality of food within the foraging range. The most sensitive parameters for monitoring the availability of food to the little penguins appear in this study to be the foraging trip duration, during both incubation and chick rearing, and the meal size delivered to the chick. In the 1995/96 season, the trips duration increased for the whole colony from a particular date which indicated that the attendance pattern was changed due to environmental conditions when food probably became less available. Chicks received 211 grams of food per day and chicks in a good breeding season received on average 35 grams more food than in a poor breeding season. These parameters integrate the effects of food availability over a very short time of perhaps 1 to 3 days and each trip is therefore a snapshot of the food available together with the foraging ability of each parent penguin. Other parameters such as chick growth rate and fledging success integrate the effects of food availability over the whole breeding season. Data of onset of breeding may reflect effects of food availability during the non-breeding period when birds are able to forage widely (Table 7.1).

Breeding period	Individual performance	Intra-seasonal	Inter-seasonal	Integration period	Factors which influence the variable
Before laying	onset of breeding	onset of breeding		weeks, breeding season	Two weeks earlier for successful breeders
Incubation	length of shifts	length of shifts		days, weeks	Shorter for successful breeders. Short, long, short throughout incubation.
	number of foraging trips		number of foraging trips	breeding season	Successful breeders make more trips. Difference between successful and failed is more pronounced in a bad season.
	foraging trip duration	foraging trip duration		days, weeks, breeding season	Shorter for successful breeders. Short, long, short throughout incubation.
Guard	length of guard		length of guard	days, weeks, breeding season	Longer for successful breeders. Longer in a good season.
Post guard			length of post guard	days, weeks, breeding season	Shorter in a good season.
	foraging trip duration	foraging trip duration	foraging trip duration	days, weeks, breeding season	Shorter for successful breeders. Increases to the whole colony as season progresses. Shorter in a good season.
	meal size	meal size		weeks	Larger for fledging chicks. Decreases from the middle to the end of the season.
		diet		weeks	Successional changes in composition as the season progresses.
			chick growth curve	breeding season	Slower growth in a bad season than the growth in a good season. Reaches the asymptotic value one week earlier in a good season.

Table 7.1   Variables which were responsive to individual, intra- and inter-seasonal variations probably caused by fluctuations in food supply.

The response of a variable to food availability should be able to be separated from a response to other factors, both biological and environmental. One of the major constraints to a monitoring program is the ability to obtain data at appropriate intervals and with sufficient accuracy. In this study, data were obtained by daily observations of nest attendance and chick weight throughout two breeding seasons. Some reproductive variables like chick growth and chick fledging weight may be influenced by factors not related directly to food supply, such as breeding age and experience, and individual variation in growth rate. Foraging trip duration measured in days was shown to be different between the good and poor breeding seasons. However, if birds spend time at sea not foraging, foraging trip duration will reflect only feeding time but not necessarily food supply. This problem when investigating food availability was partially solved by examining several variables simultaneously in different stages of the breeding cycle. Automated data collection with the Automated Penguin Monitoring System, although not fully use in this study, can provide a very large body of high-grade data in the future.

The above discussion was centred on understanding variations in little penguin breeding performance. However, a number of authors have suggested such studies also provide information on the stocks of commercial fish (eg CCAMLR 1982; Croxall et al. 1988; Furness and Barrett 1991b; Cairns 1992a; Furness et al. 1993; Montevecchi 1993; Crawford and Dyer 1995; Barrett and Krasnov 1996).

Although useful information might be obtained, such as the presence of fish of a particular species or year class, these results suggest that at present there are no clear signals reflected in the measured variables which would make the little penguin useful for providing quantitative data on specific fish stocks. Certainly variables related to foraging and breeding biology provide indirect information related to the prey (fish stocks) but such variables cannot be related directly to fish abundance in the absence of, as is now the case, independent assessment of fish stocks. The species composition of the diet of the little penguin during 1996/97 (the good breeding season for little penguin) contained virtually no anchovy or pilchard. Further the diet composition changed as the season progressed. Penguins preyed upon a temporal succession of red cod *Pseudophycis bachus*,

barracouta *Thyrsites atun*, warehou *Seriolella brama* and anchovy *Engraulis australis*. From this it may be inferred that pilchard and anchovy are not obligatory in the diet and that the little penguin is an opportunistic feeder. In addition, there is a size limit to the fish that little penguins are able to take and as some species of prey fish eg. barracouta, red cod and warehou grow they disappear from the penguin's diet. The massive mortality of pilchards which occurred in Victorian waters in March 1995 may be one if not the principal cause of breeding failure of the little penguin in the following breeding season. However there appeared to be no carry over effect into the 1996/97 breeding season when breeding success of the little penguin was at its highest and pilchards formed no part of the diet. Defining the quantitative relationship between the little penguin and its prey may be possible in the future but only if fish stock surveys are conducted at the same time as land based studies on little penguin which forage in the same zone.

The little penguin population of Phillip Island consists of some 12000 to 14000 breeding pairs which may consume the equivalent of fish taken by the entire Victorian coastal fishery. During the breeding season the penguins are confined to a limited radius of 15 km (Weavers 1992) and there is an incomplete overlap between the penguin foraging range and the commercial fishery. Outside of the breeding season the penguins range widely with a possibly greater overlap.

The fact that little penguins and the commercial fishery take the same species makes it important that a fisheries management plan be developed which takes into account the food consumption of little penguins. Pilchards and anchovies have decreased dramatically in importance in the penguin diet while the commercial catches of these fish have increased progressively. This potential competition between penguin feeding and commercial fishing has been noted previously [Hobday, 1992 #38] but it seems the implementation of measures to guarantee the future of both the food of the little penguin and a sustainable commercial fishery have been slow. The commercial fisheries are concentrated in Port Phillip Bay. There is no direct overlap between fisheries and the foraging range of Phillip Island penguins. However, there is evidence that Phillip Island region is a spawning area and contributes to the recruitment of pilchards and anchovies into Port Phillip Bay (Kailola et al. 1993; Collins et al. 1994; Hoedt et al. 1995). A

detrimental link between little penguin and pilchard/anchovy fisheries has not yet been established but waiting until over-exploitation is recognised by all parties could be proved inadequate. Ultimately it may not be possible to restore either the stock of commercially targeted fish or the depleted penguin population.

In the last 10 years, there has been a growing perception that it is not effective to base fisheries management policies only on single-species models. These target species models do not predict common events like large decadal shifts in species composition, abundance and productivity. Human-related activities such as overfishing are implicated in these fishing changes which increase pressure on top predators, like seabirds, and cause severe economic burden associated with declines in commercial fisheries. Fish population declines often lead to belated regulatory measures without a good understanding of cause and effect (Lavigne 1992). It is desirable therefore, that fishery management takes a more holistic view of the ecosystem processes. Seabirds have evolved for millions of years as small sampling units which can integrate events over a long period of time so seabird data can be used to provide information on the availability of prey. The application of these ideas needs careful consideration since at best, the measure would be one to affect the availability of prey to predator rather than the absolute abundance of prey. Nevertheless, Cairns (1992a) postulated that there are several ways to use seabird data to refine fundamental indices on fishery models such as abundance, natural mortality and recruitment rates. Foraging trip duration of penguins combined with meal mass brought ashore to the chicks could be used to estimate abundance in the same way as the catch per unit effort of fisheries science. Data on provisioning rates and penguin diet composition can refine fish natural mortality rates since natural mortality is highly variable but a constant value is always assumed in fishery assessments. Prey fish will be in the penguin diet months or years before reaching the size to be commercially harvested so penguin prey are potential predictors of subsequent recruitment to stocks of commercially harvested species. Fishery managers are now seeking to include ecosystem considerations into fishery management beyond the single species model. The differences in measured variables as response to

fluctuations of food supply indicate that little penguin data can be incorporated in a monitoring program as a potential indicator of food availability.

7.1 Conservation and further studies

This study shows the importance to determine daily the events of the life cycle of little penguins by revealing intra-seasonal fluctuations which were masked in previous studies where discontinuous period of observation was used.

Research on little penguins from Phillip Island has been conducted continuously since 1967. Several breeding sites on the island have been surveyed every year. Many published reports have emphasised the fluctuations in breeding success and related variables. There is a need, however, to establish one study site where daily monitoring can be conducted to reveal long-term trends in the within-season fluctuations of food supply.

Future studies of foraging trips during the chick rearing period should examine the duration of trips in hours. In this study, foraging trip duration was analysed in days since penguins only come ashore at dusk and leave at or just before dawn. Some birds come ashore during the night, spend one or two hours in colony and leave some hours before dawn during the reproductive season. Breeding birds during chick rearing have to travel to and from foraging areas and the analysis in hours can refine the information on foraging performance related to breeding success and reveal more about the foraging behaviour in which nocturnal little penguins have evolved.

Long term data on foraging trip duration sampled over a continuous period of time could reveal the relationship between the oceanographic current dynamics in Bass Strait and little penguin fluctuation in foraging performance. Breeding birds tended to travel longer and therefore delivered fewer meals to their chicks when the sea surface temperature (SST) of Bass Strait was greater than 20°C (Chapter 5). This increase in the SST seems to be caused by the influence of the Eastern Australian current in Bass Strait. The penguin data in this study was for two breeding seasons and long term influence of SST on the penguins' foraging behaviour could not be determined.

The mating behaviour should be taken into account in colonies where there is a potential for human interference. Changing partners and burrows between seasons decreased

reproductive success. When penguin breeding grounds are replaced by buildings, car parks, etc, and penguins are removed to new areas, it can be expected that the breeding season of removed penguins will have a later onset than birds in normal breeding conditions. As burrow and pair fidelity integrate events over a long period of time, there will probably be a negative effect in the colony even though the removal protocol is carried out in the non-breeding season period. The extent, ie the number of seasons, in which this kind of human interference will affect removed penguins is yet to be determined.

As I am writing this conclusion, December 1998, another massive pilchard mortality is occurring in the south east Australia in the same fashion as the 1995 mortality. The monitoring of diet composition of little penguins is a priority at the moment to better understand the prey-predator relationship in the ecosystem around Phillip Island and then to suggest measures of conservation. The massive mortality of pilchard in 1995 provided a natural experiment to examine the importance of this prey in the diet of little penguins. In the present study, penguins have successfully shifted to other species for one breeding season. This breeding season was, however, preceded and followed by reproductive seasons of the lowest breeding success reported in 25 breeding seasons at Phillip Island (Peter Dann, pers. comm.). Future monitoring of little penguin diet could determine the reliability of other prey species when pilchard and anchovy are unavailable.

Overall, conservation policy and management in Victorian waters adjacent to little penguin colonies will depend ultimately on the management of the fishery, particularly in the degree to which it takes into account ecosystem considerations. This management includes not only the welfare of little penguins but has implications for the local economy. The little penguin industry at Phillip Island generates three times greater revenue for the state of Victoria than the local fishery industry. It is one of the few places where the natural consumer has higher commercial value than the stock of commercially harvested species. It is mandatory to incorporate the penguin data into practical fishery management.

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Appendix 1 - Derivation of model to predict breeding success by number of foraging trip of penguins pairs during incubation[9]

As the response variable, breeding season, has only two possible values (success of failure) a Logistic Regression was used to analyse the manner in which the odds of success are related to the total number of incubation foraging trips by both parents (the explanatory variable). The Logistic regression equation relates expected breeding success (π) to the explanatory variable X_1 in the following way.

$$\ln\left(\frac{\pi}{1-\pi}\right) = B_0 + B_1 X_1$$

where B_0 and B_1 are constants to be estimated in the statistical analysis, and π is the probability of breeding success. The equation can also be expressed as

$$\pi = \frac{1}{\left(1 + \exp\{B_0 + B_1 X_1\}\right)}$$

Data for both seasons were analysed separately using the Logistic Regression procedure defined in the statistical computing package SAS as LOGISTIC. The following equations describe the relationship between the total number of incubation foraging trips for both parents and breeding success for season one and two respectively.

Logistic equation for season 1;

$$p = \frac{1}{\left(1 + \exp\{5.7721 - 0.4534 N_1\}\right)}$$

Logistic equation for season 2;

$$p = \frac{1}{\left(1 + \exp\{0.0628 - 0.0882 N_1\}\right)}$$

where p is the estimated probability of breeding success and N_1 is the total number of incubation trips by both parents. The adequacy of the logistic models was checked using the likelihood ration statistic for logistic regressions based on frequency data created from the original data set. A two factor ANOVA and LSD procedure was used to

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[9] Chiaradia, A. (2001). An incubation model to predict breeding success on Little penguins. New Zealand Journal of Zoology 28:434.

compare the mean total number of incubation foraging trips for seasons and both levels of breeding success.