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Foraging strategies and breeding success in the Little Penguin, *Eudyptula minor*: a comparative study between different habitats

by

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Little Penguins breeding at different locations in New Zealand exhibit great differences in breeding success which is likely to be related to different foraging strategies. During the 2000/2001 breeding season, foraging behaviour and breeding success of Little Penguins *Eudyptula minor* were examined at Motuara Island, Marlborough Sounds, and Oamaru, North Otago. To determine breeding success parameters and chick growth, 64 nests on Motuara Island and 87 nests at Oamaru were checked daily. On Motuara Island an average of 0.71 chicks fledged per pair, which was significantly lower than the 1.44 chicks per pair recorded at Oamaru. Breeding failure on Motuara Island was generally related to weather conditions or chick starvation and appeared during two distinct periods. At Oamaru, predation was the main mortality factor.

VHF-telemetry (‘Radio tracking’) was used to determine foraging ranges and at-sea behaviour of penguins equipped with streamlined transmitter packs. Motuara Island penguins rarely left the Queen Charlotte Sound on one-day trips, staying close to the Island (maximum distance to colony or foraging radius < 9 km) and travelling relatively short distances (mean = 24.4 km). Birds that did leave the Sound generally stayed away for at least 2 days (long-term trip). In contrast, Oamaru penguins showed a much wider foraging range (foraging radius < 30 km) and travelled greater distances (mean = 57.4 km) during one-day trips. At Motuara Island, long-term trips occurred during incubation and chick rearing, but at Oamaru, penguins did not make long-term trips (>1 day) after the chicks hatched.

Five birds on Motuara Island and 6 birds at Oamaru were equipped with time-depth recorders (TDRs) to investigate diving performance. Compared to Oamaru, penguins from Motuara Island showed a greater number of dives per trip (mean number of dives 1165 vs. 809), dived significantly deeper (mean depth 10.1 vs. 6.0 m) and longer (mean dive duration 29.5 vs. 22.4 seconds). Comparison of dive parameters suggest that penguins from Motuara Island search for prey in greater parts of the water column (depths <26 m) than penguins at Oamaru (depths <14 m).

The main factors influencing the foraging behaviour of Motuara Island penguins are probably temporary variations in prey availability and foraging restrictions by topographic features of Queen Charlotte Sound. Oamaru penguins have a much wider area in which to forage: environmental constraints (bathymetry, coastal topography) seem to have little effect on breeding success and foraging behaviour is probably determined mainly by prey distribution.
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Chapter 1

General Introduction

1.1 RATIONALE

Penguins (family: Spheniscidae) are a unique family of flightless pelagic seabirds that are common in cooler waters of the southern hemisphere (Reilly 1994). Penguins live between two worlds: they feed exclusively at sea but must return to land to breed. Some penguin species are known to spend as much as 80% of their lifetime at sea and only return to land during the breeding season (Williams 1995).

During the breeding season, nest duties limit the time to forage and thus are likely to affect the foraging ranges of penguins. Especially after the chicks have hatched, it is crucial that the adult birds find enough food within a short period of time and return to feed their chicks regularly (Wilson 1995). In the later stages of chick rearing, the adult penguins may have to increase their foraging efforts to match the growing demand of their offspring (e.g. Davis et al. 1989, Gales & Green 1990, Culik 1994). This is generally achieved by extending the foraging ranges - the birds travel further away from their colonies and cover greater distances during foraging trips (Bethge et al. 1997, Radl & Culik 1999).

In this light, it is clear that the prey availability in relatively close proximity to the breeding sites plays an important role in determining the reproductive success of penguins. Little Penguins (Eudyptula minor), the smallest of all extant penguin species, are widely distributed around New Zealand, Tasmania and Southern Australia (Reilly & Cullen 1981). Little Penguins breeding on Motuara Island, Marlborough Sounds (41°06'S, 174°16'E) in the north of New Zealand’s south island, exhibited poor breeding success rates in recent years (Renner 1998, Numata 2000). Renner recorded high chick mortalities and related these to a sudden pilchard (Sardinops neopilchardus) die-off in the Marlborough Sounds. He suggested that the resulting prey scarcity forced adult penguins to make much longer foraging trips that subsequently led to nest desertions and chick starvation. However, 2 years later Numata et al. (2000) also recorded a comparably low breeding success on Motuara Island, that was presumably related to prey scarcity, but without any evidence that a drastic event like a mass
die-off occurred. The main reason for the low breeding success was again prolonged foraging trips that led to nest desertions (Numata et al. 2000).

A comparison of nest attendance patterns and breeding success of Little Penguins from Motuara Island with conspecifics breeding 600 km south at Oamaru, North Otago (45°06'S, 174°16'E) revealed remarkable differences between both populations. During the last decade, Little Penguins at Oamaru have exhibited some of the highest breeding success rates recorded for that species (D. Houston, pers. comm.). Numata et al. (2000) found that there was a close relationship between the length of foraging trips and the breeding success. The foraging trips of Little Penguins from Oamaru were significantly shorter than those recorded at Motuara Island, nest desertions and chick starvation were practically non-existent at Oamaru.

Considering this, the close relationship between prey availability, foraging behaviour and breeding success is apparent. Poor food conditions force Little Penguins to increase their foraging effort. As a result the penguins may have to stay longer at sea to obtain enough food before returning to their nests. This in turn increases the possibility of nest desertions of adults and chick starvation (Renner 1998, Numata 2000). The reproductive outcome can, therefore, be considered as an indicator of possible major differences in the foraging behaviour of Little Penguins from Motuara Island and Oamaru.

Based on this assumption, the aim of this study was to examine differences in the at-sea behaviour of Little Penguins from Motuara Island and Oamaru. Where do the birds go on foraging trips during the breeding season? How do the foraging ranges differ between both sites? Are there differences in diving performance between sites and how can these differences be related to prey availability and distribution? What factors may influence differences in foraging behaviour? And, can foraging behaviour be related to environmental features at both sites?

The at-sea behaviour of penguins is notoriously hard to study. Since visual observations are virtually impossible (but see Dann 1989), the only way to get information is the use of telemetric methods or the deployment of data loggers. ‘Radiotelemetry’ – the tracking of VHF transmitters attached to penguins via land based receiving stations – was used to determine foraging routes and ranges that were undertaken by individual breeding Little Penguins at both locations. To get more insight on the actual diving behaviour, data loggers were deployed that recorded depth, temperature and light level at certain time intervals.
Additionally breeding parameters (chick growth, breeding success) were recorded to determine the differences in breeding success of Little Penguins on Motuara Island and at Oamaru.

1.2 STRUCTURE OF THE THESIS

This thesis consists of independent Chapters that are intended for publication in international journals and are written in the form of scientific papers. Therefore, some overlap in the Introduction and Material and Methods sections of each chapter may occur. The overall structure of the thesis is as follows:

Chapter 1 outlines the rationale and the main questions on which this study was based.

Chapter 2 gives an overview of the study area and briefly describes environmental features and breeding conditions of the sampling sites.

Chapter 3 focuses on differences in foraging ranges and movements at sea between both sites with respect to breeding success.

Chapter 4 describes differences in diving behaviour of Little Penguins breeding on Motuara Island and at Oamaru.

Chapter 5 presents the conclusion to this project.
1.3 REFERENCES


Chapter 2

Study areas

The study was conducted at two sites on New Zealand's South Island: on Motuara Island, Marlborough Sounds (51°06'S, 174°16'E) and at Oamaru, North Otago (45°06'S, 170°58'E – Fig. 2.1). All data sampling took place during the Little Penguin’s breeding season 2000/2001 and was divided into three phases starting with test runs of the telemetry equipment at Oamaru (3.7.2000 – 26.8.2000), three months of data collection on Motuara Island (6.9.2000 – 29.11.2000) and finally 7 weeks of data collection at Oamaru (4.12.2000 – 21.1.2001).

2.1 MOTUARA ISLAND

Motuara Island is a small island of 59 hectares located in the outer Queen Charlotte Sound (Fig. 2.1). Average water depths in the outer Queen Charlotte Sound are approximately 30m. At the Sound entrance (roughly the line Cape Koamaru – Cape Jackson) the water depth drops sharply to more than 100m in Cook Strait. Depths in the inner Queen Charlotte Sound increase to >60m south of Long Island. Currents inside Queen Charlotte Sound are mainly restricted to tidal water movements. However, a strong south-eastward current is present in Cook Strait just outside Queen Charlotte Sound.

Little Penguins on Motuara Island breed in different areas (mainly gullies leading to the sea) that are widespread across the island. Different types of burrows are used by the birds ranging from the occasional open nest to hollow trees, earth burrows, caves or crevasses in rocky outcrops and nest boxes installed by the Department of Conservation (DoC). Nests generally are distributed from sea level up to the highest points of the main ridge with the majority of burrows at lower elevations. Other burrow breeding seabirds on the Island are Sooty shearwaters (Puffinus griseus) and Fluttering shearwaters (Puffinus weis) and competition for burrows with Little Penguins is common (Renner 1998, pers. observ.).

Renner (1998) estimated that the breeding population of Little Penguins on Motuara Island consists of approximately 300 pairs. However, at the time of this study the numbers of breeding pairs appeared to be considerably less. Most of the burrows examined by Renner were unoccupied and finding occupied nests was difficult. Active nests were found by
searching during the first week on Motuara Island. Nest locations were recorded with a maximum position error of 10 m using a GPS receiver (Garmin GPSII Plus). The distribution of the sampling areas and nest positions is given in Figure 2.2.

2.2 OAMARU

Oamaru is located on the east coast of the South Island about 20 km south of the Waitaki River estuary (Fig. 2.1). The sea off the North Otago coast is moderately shallow and the 50 m depth contour is found some 30 to 50 km offshore. A consistent northward current follows the coastline towards Banks Peninsula in Canterbury.

Penguins breed all along the rocky foreshore of Oamaru. The study sites at Oamaru consisted of two breeding areas that are separated by the Oamaru harbour. The Oamaru Blue Penguin Colony (OBPC) uses the premises of a former Quarry at the eastern side of the Oamaru harbour and consists of a row of artificial hills with about 200 dug-in nest boxes with removable lids (“Quarry” – Fig. 2.3). The nest box area is surrounded by a closed fence to reduce disturbance of the penguins by people and to keep out dogs and sealions (Phocarctos hookeri). The mesh size of the fence is big enough to let penguins slip through it without problems. The Oamaru Blue Penguin Refuge (OBPR) is a second fenced nest box area between the Oamaru Creek and the northern end of the Oamaru harbour and is closed to the public (“Creek” – Fig. 2.3). The OBPR also consist of artificial breeding hills with nest boxes and is fenced off on three sides with the unfenced side only protected by a row of thick bush facing the beach.

To reduce the impact of predators like cats, Norwegian rats (Rattus norvegicus) or ferrets (Mustela furo) inside the nest area, an array of tunnel traps is set permanently in both areas (D. Houston, pers. comm.).
Figure 2.1 Overview of the study areas: (A) Marlborough Sounds and Cook Strait, (B) outer Queen Charlotte Sound (SC – Ship Cove, CC – Cannibal Cove) and (C) Oamaru, North Otago
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Chapter 3

Foraging ranges and breeding success in Little Penguins (*Eudyptula minor*): a comparison of two breeding populations in New Zealand

3.1 INTRODUCTION

Foraging ranges of penguins and other seabirds are dictated mainly by prey availability and the stage of breeding. Prey availability is affected by environmental and climatic variables (Tveraa *et al.* 1997, Hull *et al.* 1997, Culik *et al.* 2000) and varies between regions depending on ecological conditions (e.g. productivity, oceanic conditions) (Boersma *et al.* 1990, Radl & Culik 1999). Outside the breeding period, penguins can be relatively independent of their breeding colonies and may undertake longer foraging trips (Weavers 1992, Wilson 1995, Wilson & Culik 1998). During the breeding period, however, foraging ranges of the adults are greatly reduced by the increasing energetic demands of their chicks which force the parents to return to their nest frequently to feed the chicks (Wilson 1995, Hull 2000).

Variations in prey availability require behavioural responses by penguins. Since the probability of prey encounters increases with the total distance travelled, penguins might try to compensate for prey scarcity with longer foraging trips that may take them further away from their colony (Wilson & Wilson 1990, Radl & Culik 1999). If low foraging success forces breeding penguins to undertake prolonged foraging trips the probability of nest failure and chick starvation is increased (Davis 1982, Boersma *et al.* 1990, Watanuki *et al.* 1993, Numata *et al.* 2000). Considering this it is apparent that the reproductive success depends greatly on food availability in close proximity to the nest site (Davis *et al.* 1989, Gales & Green 1990, Watanuki *et al.* 1993).

Studies of Little Penguins (*Eudyptula minor*) in New Zealand found strong relations between short term variations in prey availability and breeding success. Renner (1998) suggested that the low breeding success recorded for Little Penguins on Motuara Island/Marlborough Sounds might have been the result of a sudden pilchard die-off during the breeding period. A comparative study between penguins on Motuara Island and conspecifics breeding 600 km south at Oamaru revealed correlations between breeding success and foraging trip durations.
(Numata et al. 2000). The birds on Motuara Island stayed significantly longer at sea, which resulted in high rates of egg desertion and chick starvation, resulting in a much lower breeding success than recorded for birds at Oamaru.

These findings underline the strong relationship between prey availability, foraging range and breeding success. It seems that penguins from Motuara Island have to cope with time dependent variations in prey availability and are more likely to face food shortage close to their breeding sites. These variations seem to force the birds to go on longer foraging trips during the breeding period which may be the reason for their poor breeding success. In contrast, Little Penguins breeding at Oamaru are known to have some of the best reproductive success rates on record (Numata et al. 2000, Perrimen & Steen 2000, D. Houston, pers. comm.). This is likely to be due to year-round stable availability of a single prey species that provides enough food within close range of the breeding sites (Fraser 1999, M. McGregor, pers. comm.).

Using VHF telemetry, I set out to compare the foraging behaviour of Little Penguin populations breeding at Oamaru and Motuara Island. Both locations differ greatly in geographic and oceanographic features which may have a considerable impact on the foraging behaviour of the local populations. I examined how the foraging behaviour differed between both populations and tried to determine which factors caused these differences. Finally, breeding success was recorded to assess how reproduction and foraging are related at both locations.
Chapter 3: Foraging ranges and breeding success

3.2 MATERIALS AND METHODS

This study was conducted during the breeding season 2000/2001 on Motuara Island (41°06'S, 174°16'E) in Queen Charlotte Sound and at Oamaru (45°06'S, 170°58'E) in Otago. A detailed description of both study areas is given in Chapter 2. Field work started in Oamaru (3.7.2000 – 26.8.2000), was continued on Motuara Island (6.9.2000 – 28.11.2000) and then ended with a second period in Oamaru (4.12.2000 – 21.1.2001). I used streamlined (Bannasch et al. 1994) transmitters comprising of MiPs-1B transmitter cores (Reimesch Kommunikationssysteme, Bergisch Gladbach, Germany). The transmitters' dimensions were 60 x 20 x 18mm; the devices weighed 35 grams. The transmitters emitted 60 to 80 pulses per minute depending on battery voltage and dampness. Signals were passed through a 23 cm long aerial which was designed to break the surface as soon as the penguin emerged. The devices were attached to the feathers of the penguins' lower back (Bannasch et al. 1994) with black adhesive tape (No. 4651, TESA Baiersdorf AG, Hamburg, Germany) using a technique described by Wilson et al. (1997). The attachment procedure lasted approximately 15 minutes per penguin.

Transmitters were fitted to 20 penguins at Oamaru (8 and 12 birds during the first and second period respectively) and 14 penguins at Motuara Island. All but one penguin (at Oamaru) were breeding birds, either on eggs or with chicks. Generally transmitters were recovered after one foraging trip. However, especially on Motuara Island, birds sometimes managed to elude recapture and undertook more foraging trips before their devices could be recovered. Four penguins (two at Oamaru and two on Motuara Island) failed to return to their nests and the transmitters could not be recovered. On Motuara Island, two birds abandoned their nests but were recaptured to remove the devices. The causes of breeding failure were unknown and may have been due to handling or the impact of the transmitters. However, in at least two cases the influence of predators may have played a role. Unrecovered transmitters would have fallen off at moultling.

Signals were received using two pairs of directional receiving antennas (RA-NS 5, Telonics, AZ, USA) that were installed in a "null peak" array configuration and were attached to vertical, revolving masts (height: 3m). The signals were passed through coaxial cables to a Yeasu FT-290 RII transceiver that was powered by a solar panel. Depending on the signal strength an ULNPA 150 pre-amplifier (Reimesch Kommunikationssysteme, Bergisch Gladbach, Germany) was connected between antenna and transceiver. At Oamaru the
receiving stations were set up along the coastline at elevations of 22 m and 61 m respectively; the distance between both stations (baseline) was 11.7 km. At Motuara Island the antenna arrays were positioned on the island’s highest point (148 m) and on Arapawa Island, at the eastern side of Queen Charlotte Sound, at 426 m; the length of the baseline was 7.9 km. Considering the elevation of the receiving stations, I estimated the maximum reception range to be 20 to 30 km at Oamaru (“straight-line signal propagation” – distance antenna/horizon) and approximately 40 km at Motuara Island (transmitter’s maximal range). Further limitations of reception at Motuara Island resulted from topographic features such as islands, bays and hills that either caused areas of radio shadow or reflected and subsequently scattered the signal so that accurate bearings were sometimes difficult to obtain. Lastly, signal transmission was interrupted whenever the birds were diving.

All antenna operators passed an introductory workshop during which they had to take bearings on stationary signals with known positions. From these tests I was able to estimate the mean error of bearings at ±1.5° (see Appendix I for further details on assessment of location errors). Penguins were tracked from sunrise to sunset (10 to 14 hours per day). On some days the tracking was delayed or had to be aborted due to unfavourable weather conditions. Bearings on birds were recorded in 10 minute or 15 minute intervals depending upon the number of birds at sea. Both receiving stations were in constant contact (VHF-radios or cellphones) to compare bearings and check for error.

The birds’ positions were calculated and plotted from the directional data using Matlab for Windows (Version 5, Mathworks, Inc.). Position fixes accepted after data analysis, were used to calculate foraging range parameters. I defined the “mean foraging radius” as the mean distance between nest site and all position fixes obtained for a single foraging trip. The “maximal foraging radius” describes the maximum distance from the colony reached by a penguin during one trip. The “total distance travelled” is the sum of distances between all consecutive position fixes of single trips and includes the direct (linear) distances between nest site and first position fix and last position fix. “Travelling speed” describes the horizontal swimming speed a penguin must have swum between consecutive position fixes; horizontal speeds < 0.36 km/h (~0.1 m/s) were regarded as drifting (Culik et al. 1998) and therefore rejected. “Travelling speeds” should not be mistaken for actual swimming speeds, since the vertical component of the penguins’ movements is not included. For statistical comparison
individual means of all foraging parameters were used. Foraging trips with less than seven position fixes were not included.

In general, two different types of foraging trips were distinguished at both study sites. Especially during the incubation phase the penguins often stayed at sea for at least two days. I defined these over-night trips as long-term trips. After the chicks had hatched, one-day foraging trips were common; the adults left the nest in the early morning hours and returned on the evening of the same day to feed their offspring. I termed these one-day trips.

A detailed description of the above summarized techniques (transmitter design, attachment methods, error assessment, data analysis) is given in Appendix I.

In both study areas I determined breeding success and chick growth. On Motuara Island a total of 57 active nests were found during the first week of the field work. At Oamaru, all 64 nest boxes that were occupied on the first day of the field work were included. At both sites, breeding stages on the first day of data collection ranged from the early incubation phase to the post-guard stage. I conducted daily nest checks during which breeding status (number of eggs, number of chicks) was recorded. Additionally, the identities of adult birds (if present) were determined. Some penguins on Motuara Island had been tagged during previous studies using subcutaneous TIRIS transponders (Renner 1998). If both individuals of a breeding pair were untagged I used stainless steel flipper bands on one bird. In Oamaru all penguins were tagged with flipper bands.

All adult penguins were sexed using bill dimensions (Gales 1988). The nest checks provided several breeding success parameters that were later used to compare breeding success between study areas: number of eggs per pair, number of chicks hatched per pair, number of chicks fledged per pair, number of chicks hatched per number of eggs laid ("hatching success"), number of chicks fledged per number of chicks hatched ("fledge success") and number of chicks fledged per number of eggs laid ("breeding success").

Furthermore, where possible I determined the causes of hatching failure of eggs and fledging failure of chicks. I defined five different categories of hatching failure: "nest desertion by parents", "weather effects" (e.g. flooded burrows), "egg broken", "egg out of nest", and if the cause of hatching failure was unclear, I defined the egg fate as unknown. To classify the
causes of fledging failure six different definitions were used: starvation (when chicks had shown significant loss of body weight), nest desertion (one or both parents abandoned nest, generally leads to starvation), weather effects (e.g. flooding of burrows), predation, unknown (chicks died of unknown causes) and disappearance (chicks disappeared from burrow but did not necessarily die). I determined chick growth rates and fledging ages. On Motuara Island, chicks were weighed every five days using cotton bags and spring balances (±2 g and ±10 g). In Oamaru, chick weights were recorded during the weekly nest monitoring conducted by staff of the Oamaru Blue Penguin Colony. Linear regression of chick weights was used to estimate approximate hatch dates in nests that were found after the chicks had hatched. This method was validated by testing it on all chicks with known hatch date and was found to be 99% accurate when used on chicks that weighed less than 300 g when first found. At Oamaru hatch dates could be estimated for all nests. On Motuara Island 28 nests were found after chicks had hatched; hatch dates could be estimated for chicks in seven nests. Therefore, I was able to determine fledge ages of chicks in 43 different nests.

Statistical analysis was carried out in Minitab for Windows (Version 13, Minitab Inc. PA, USA). All means are presented with ± 1 standard deviation. For comparisons between study areas with respect to foraging (individual means) and breeding success Student’s t-test was used to test for significant differences if the samples proved to be normally distributed (Kolmogorov-Smirnov/Lillefors-test for normality). Individual differences in foraging parameters of the penguins were compared using the non-parametric Kruskal-Wallis H-test. To find appropriate models for chick growth rates Curve Expert 1.3 (D. Hyams 2001, http://www.ebicom.net/~dhyams/cvxpt.htm) was used. This software uses up to 30 different curve functions and gives a ranking of the best fitting models for a set of data (e.g. chick weights). Significance was set at the $\alpha = 0.05$ level.
3.3 RESULTS

Foraging trip types and foraging ranges

Long-term trips

Most long-term trips could not be fully reconstructed because birds swam beyond the maximum receiving range. Therefore, most of the information about long-term trips is restricted to the first day of the penguins' trips; in a few cases a penguin's signal was picked up again on the day it returned.

At Oamaru, four long-term trips were partially recorded for four different birds (three incubating birds, one non-breeder). The penguins generally travelled with the coastal current northwards on an inshore course parallel to the coastline and stayed in waters of less than 20 m depth (Fig. 3.1). Two of the three breeding birds failed to return to their nests. The non-breeding bird travelled south but stayed in shallow waters within receiving range until returning to the colony after three days; the third day of this trip could not be tracked due to a storm. It seems that long-term trips are only common during the incubation phase; no penguin with chicks was recorded making a long-term trip.

This was different on Motuara Island where six long-term trips were recorded for six different penguins. Of those, two birds were tending chicks and left their nest for 2 days and 7 days respectively, the chicks in both nests were between 4 and 6 weeks old. All birds on long-term trips left Queen Charlotte Sound (Fig. 3.2). The penguins either chose an offshore course into Cook Strait swimming into the prevailing northwest winds and roughly following the 100m depth contour (three birds) or stayed in an area of 50 to 100 m deep waters north-west to north-east of Cape Jackson (two birds). Only one bird travelled on an inshore course swimming southwards along the eastern shores of Arapawa Island.

One-day trips

At Oamaru a total of 13 one-day trips made by nine different birds (one incubating eggs, eight rearing chicks) were recorded in a 3 week period in December. On Motuara Island I was able to track six penguins on a total of 10 one-day trips.

The foraging ranges of penguins from Oamaru recorded on one-day trips varied considerably between individuals that were at sea on the same day, as well as between foraging trips that
were made by a single penguin on two different days. Some penguins stayed close to their nest sites all day and seemed to forage within confined areas close to their colonies (foraging radius <15 km - Fig 3.3). On other occasions penguins spent most of the day travelling and covered larger distances on linear or circular paths (foraging radius >15 km - Fig 3.4). In contrast, penguins from Motuara Island rarely crossed the 50m depth contour at the entrance of Queen Charlotte Sound and therefore stayed relatively close to the island all day (Fig.3.5). Ninety-five percent of all positions were located in waters not deeper than 30 m. Only one bird left the Sound eastwards into Cook Strait and returned on the same day.

At Oamaru penguins travelled within a mean radius of 10.8 km (S.D = 4.5 km, range = 4.5 - 17.8 km, n = 9) and reached maximum distances to their nest sites (max. foraging radius) ranging from 6.4 km to 30.4 km (mean = 19.2 km, S.D. = 7.7 km, n = 9). Penguins from Motuara Island showed a far more limited mean radius of only 3.1 km (S.D. = 2.1 km, range = 1.4 - 6.9 km, n = 6) and the maximum foraging radii, which ranged from 2.7 to 8.8 km (mean = 4.9 km, S.D. = 2.3, n = 6), did not exceed the distance from the island to the entrance of Queen Charlotte Sound (~9 km). The different foraging ranges between both sites are apparent when the distribution of all recorded penguin positions with respect to the distance to the nest sites is considered (Fig. 3.6). Differences in foraging parameters proved to be significant (t-tests: mean foraging radius, \( t_{13} = 3.89, p < 0.005 \); maximum foraging radius, \( t_{13} = 4.37, p < 0.001 \)).

Little Penguins from Oamaru on one-day trips covered distances between 35.5 and 75.5 km (mean = 57.4, S.D. = 14.8, n = 9) km day\(^{-1}\); at Motuara Island, on the other hand, the distances swum during one-day trips were much shorter and averaged 24.4 km (S.D. = 2.5 km, range = 20.7 km - 27.7 km, n = 6). As a result, Little Penguins from Oamaru travelled significantly longer distances (\( t_{13} = 5.34, p < 0.001 \)).

At both sites there were no significant correlations between chick age and mean foraging radius (Oamaru: \( r = -0.21, p = 0.512 \); Motuara Island: \( r = -0.519, p = 0.232 \)) or chick age and total distance travelled (Oamaru: \( r = 0.08, p = 0.804 \); Motuara Island: \( r = 0.634, p = 0.126 \)). Furthermore, no significant differences in foraging parameters were found between sexes at Oamaru (2 females vs. 7 males, \( t\)-test: mean foraging radius, \( t_{7} = -0.80, p > 0.05 \); total distance travelled, \( t_{7} = -1.71, p > 0.05 \)) or Motuara Island (2 females vs. 4 males, \( t\)-test: mean foraging radius, \( t_{4} = 0.98, p > 0.05 \); total distance travelled, \( t_{4} = -2.27, p > 0.05 \)).
Swimming speeds

Little Penguins leaving on long-term trips at Oamaru and Motuara Island showed comparable individual mean travelling speeds with no statistically significant difference between the two sites (Oamaru: mean = 4.1 km/h, S.D. = 0.3 km/h, range = 3.9 - 4.4 km/h, n = 4; Motuara Island: mean = 4.5 km/h, S.D. = 1.1 km/h, range =3.4 - 6.4 km/h, n = 7; t-test: $t_9 = -0.52$, $p > 0.05$). On short-term (one-day) trips birds from Oamaru displayed mean speeds ranging from 2.1 - 4.6 km/h (mean = 3.4 km/h, S.D. = 0.9 km/h, n = 9). Travelling speeds recorded for Little Penguins from Motuara Island averaged 2.5 km/h (S.D. = 0.6 km/h, range = 1.9 – 3.4 km/h, n = 6) and were significantly slower than those recorded at Oamaru (t-test: $t_{13} = -13.68$, $p < 0.001$).

Considering the different foraging patterns on one-day trips (short-range or long-range trips) that were observed at Oamaru, speed differences between individuals were predictable and, indeed, proved to be statistically significant (Kruskal-Wallis H-test: $df = 8$, $H = 62.66$, $p < 0.001$). The same was true for Motuara Island, when speed differences between all penguins on one-day trips were compared (Kruskal-Wallis H-test: $df = 5$, $H = 32.15$, $p < 0.001$). However, if speeds were excluded for the one bird that left Queen Charlotte Sound on a one-day trip, the speed differences between individuals were no longer significant (Kruskal-Wallis H-test: $df = 4$, $H = 6.98$, $p > 0.05$).

On long-term trips the main travelling speeds recorded at both sites lay in comparable speed ranges between 1 and 4 km/h and showed no striking differences (Wilcoxon test for paired comparisons, 1km/h speed classes: n = 12, Z = 0.08, p = 0.47 - Fig. 3.7). On one-day trips differences in horizontal travelling speeds were apparent but did not differ significantly (Wilcoxon test: n =12, Z = 0 -0.78, p = 0.22). At Oamaru penguins travelled in speed ranges from 1 to 6 km/h with the modal speed being in the 2 km/h speed class; speeds up to 8 km/h were not unusual. Birds from Motuara Island, however, generally did not travel faster than 4 km/h, with most speeds between 0 and 3 km/h; speeds higher than 5 km/h were uncommon (Fig.3.7).
Figure 3.1  Long-term trip of Little Penguin 22873 (female, 2 eggs) on 11.08.2000, Oamaru. The bird travelled northwards parallel to the coastline. After 16:20 hrs only the northern receiving station was able to track the bird’s course. The arrow indicates the further travel direction. The bird returned 8 days later but failed to relieve its partner and abandoned the nest. Dashed lines connect positions that were recorded more than 15 minutes apart.
Figure 3.2  Long-term trip of Little Penguin HG03-445 (female, 2 eggs) on 17.09.2000, Motuara Island. The bird left Queen Charlotte Sound and travelled due north-north-east roughly following the 100m depth contour. It returned 6 days later to feed its chicks that had hatched on the day of its return. Dashed lines connect positions that were recorded more than 10 minutes apart.
Figure 3.3 One-day trip of Little Penguin 26610 (male, 1 chick) on 11.12.2000, Oamaru. The birds stayed in short-range of its nest site and covered a total travel distance of 35.5 km day$^{-1}$. It reached its maximum distance to the colony (max. foraging radius: 6.9 km) at 16:45 hrs. Dashed lines connect positions that were recorded more than 15 minutes apart.
Figure 3.4 One-day trip of Little Penguin 26237 (male, 1 chick) on 13.12.2000, Oamaru. The bird travelled on a linear long-ranged course. The total distance it covered during this trip was 75.5 km day$^{-1}$; the maximum distance to the colony was reached at 11:45 hrs. Dashed lines connect positions that were recorded more than 15 minutes apart.
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Figure 3.5  One-day trip of Little Penguin HG02-484 (male, 2 eggs) on 07.09.2000, Motuara Island. The bird rarely crossed the 50 m depth contour and stayed mainly in shallower waters of Queen Charlotte Sound. It travelled a total distance of 30.6 km day$^{-1}$ and reached its maximum distance to the colony (max. foraging radius: 9.2 km) at 09:30 hrs. Dashed lines connect positions that were recorded more than 10 minutes apart.
Figure 3.6 Area utilization by Little Penguins on one-day trips: frequency distribution of pooled foraging radii (distance between all obtained penguin positions and colony) recorded at Oamaru (black bars: n = 474, 9 birds) and on Motuara Island (grey bars: n = 450, 6 birds). More than 50% of all penguin positions recorded on Motuara Island were within a range of 4 km of their nest sites; 95% of all position fixes were within 8 km of the penguins’ burrows. In contrast, position fixes for Oamaru birds were spread over a much wider range of distances with 50% of all recorded foraging radii being greater than 8 km.
Figure 3.7  Frequency distribution of horizontal travelling speeds recorded for Little Penguins from Oamaru and Motuara Island on long-term and one-day trips. All speed data resulted from distances between consecutive position fixes that were generally recorded in 10 or 15 Minute intervals.
Breeding success

Causes of hatching failure

In Oamaru 128 eggs were found in 64 nests. Twenty-seven eggs in 25 different nests failed to produce chicks. On Motuara Island a total of 115 eggs were found in 57 nests. No chicks hatched from 28 eggs in 17 different nests.

Of the 27 unsuccessful eggs recorded at Oamaru, 18 (66.7%) did not hatch for unknown reasons (Fig. 3.8). Five eggs (18.5%) were found outside nest boxes. Two eggs (7.4%, in one nest) did not result in chicks due to nest desertion and another two eggs (7.4%, in two different nests) were found broken. On Motuara Island 46.4% of all causes of hatching failure (13 eggs) were related to nest desertions (Fig. 3.8). Four eggs were found outside the nest (17.9%) and further four eggs were broken (14.3%). In one nest no chicks hatched out of two eggs (7.1%) because of weather influences (burrow completely flooded). In four nests one of two eggs was unsuccessful for unknown reasons (14.3%).

Causes of fledging failure

In Oamaru 101 chicks hatched, 19 of these did not fledge (Fig. 3.9). Ten of these chicks (52.6%) disappeared from their nests and their fate could not be determined. In one night eight chicks (42.1%) were killed by stray dogs. One chick (5.3%) died for unknown reasons.

On Motuara Island 87 chicks hatched but only 40 fledged. Twelve chicks (25.5%) died although their parents returned to their nest frequently. Those chicks all lost weight until they died which indicates that the parents failed to feed their chicks adequately. Another 12 chicks (25.5%) died because their parents failed to return to their nests which subsequently led to the death of the chicks (12 chicks, 25.5% - Fig. 3.9). In a period of heavy rain that flooded the burrows six chicks (12.8%) either drowned or died of hypothermia. The causes of death for 10 chicks could not be determined. Seven chicks disappeared but in two cases predation by Weka (Gallirallus australis) seemed likely.

Chick growth

Chick growth curves (body mass against age) in both colonies differed greatly. At Oamaru the logistic growth model would have been the best to fit growth curves for first and second hatched chicks (A- and B-chicks); polynomial function ranked fifth in Curve Expert. The only function to fit growth curves appropriately for A- and B-chicks on Motuara Island were fifth
degree polynomial functions. Therefore this function was used for chick growth at both study sites (Fig. 3.10). Chick growth at Oamaru appeared linearly during the first 30 days after hatching, followed by a period of reduced mass gain until the 45th day before the chicks started slightly to loose mass until fledging. At Motuara Island, there seemed to be a slower mass gain in the first 10 days, before a period of nearly linear growth set in. The linear increase started to decline between the 25th (B-chicks) and 30th (A-chick) days after hatching. From the 40th day onwards mass gain levelled out for A-chicks and even showed slight decrease for B-chicks, before finally increasing again for both chicks until fledging.

Weights of all chicks between 10 and 20 days of age at Oamaru ranged from 200 to 800 g (n = 147, mean = 449.6 g, S.D. = 126.2 g); on Motuara Island chicks of the same age class weighed only between 160 and 635 g (n = 50, mean = 375.5 g, S.D. = 120.3 g). This difference proved to be significant (t195 = -3.63, p < 0.001). Even more striking differences could be observed for all chicks in the age class of 40 to 50 days. In Oamaru chicks of that age had a mean body mass of 1132 ± 120 g whereas conspecifics of the same age on Motuara Island had a mean body mass of only 816 ± 208 g; this difference was highly significant (t183 = -12.59, p < 0.001). Mean fledging weights for all chicks were 1099.1 ± 132 g in Oamaru and significantly lower with a mean of 946.8 ± 154 g on Motuara Island (t123 = -5.53, p < 0.001). Fledge ages also differed significantly between both locations (Oamaru: 57 ± 2 days, Motuara Island: 66 ± 6 days; t97 = -5.76, p < 0.001).

Breeding success

A comparison of breeding parameters is given in Table 3.1. There was no significant difference in number of hatched chicks per pair and hatching success. However, all other parameter differences were significant. In Oamaru 87% of all chicks survived until fledging despite the fact that several chicks were killed by dogs during the last night of this study. On Motuara Island only 47% of all hatched chicks survived. The overall breeding success of Little Penguins breeding in Oamaru was much higher than on Motuara Island (Table 3.2). In Oamaru the breeding success determined for nests with radio-tagged birds (1.27 ± 0.47, n = 14) was lower than in control nests (1.72 ± 1.14, n = 67) but not significantly so (t79 = -1.27, p > 0.05). On Motuara Island the breeding success for nests with equipped birds (1.09 ± 0.9, n = 15) was higher than in control nests (0.56 ± 0.79, n = 34); but again this difference was not significant (t47 = 1.91, p > 0.05).
Table 3.1 Breeding parameters and breeding success of Little Penguins in Oamaru and on Motuara Island. All parameters are displayed as means ± standard deviation, number of observations in parentheses.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Oamaru</th>
<th>Motuara Island</th>
<th>( t )</th>
<th>d.f.</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of eggs per pair</td>
<td>2.00 ± 0.00</td>
<td>2.02 ± 0.44</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>(64)</td>
<td>(56)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of chicks hatched per pair</td>
<td>1.67 ± 0.58</td>
<td>1.53 ± 0.77</td>
<td>0.78</td>
<td>96</td>
<td>0.436 *</td>
</tr>
<tr>
<td></td>
<td>(64)</td>
<td>(56)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of chicks fledged per pair</td>
<td>1.59 ± 1.18</td>
<td>0.70 ± 0.82</td>
<td>3.95</td>
<td>96</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>(64)</td>
<td>(56)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatching success</td>
<td>0.84 ± 0.37</td>
<td>0.76 ± 0.43</td>
<td>1.45</td>
<td>239</td>
<td>0.148 *</td>
</tr>
<tr>
<td>No. of chicks hatched per no. of eggs</td>
<td>(128)</td>
<td>(113)</td>
<td></td>
<td></td>
<td></td>
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<td>Fledging success</td>
<td>0.84 ± 0.39</td>
<td>0.47 ± 0.50</td>
<td>4.11</td>
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<td>No. of chicks fledged per no. of chicks hatched</td>
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<td>(86)</td>
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<td>Breeding success</td>
<td>0.72 ± 0.45</td>
<td>0.35 ± 0.48</td>
<td>6.07</td>
<td>239</td>
<td>&lt; 0.001</td>
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<tr>
<td>No. of chicks fledged per no. of eggs</td>
<td>(128)</td>
<td>(113)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* indicates no significant difference
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Figure 3.8 Causes of egg failure determined for Little Penguins breeding on Motuara Island and at Oamaru.

Figure 3.9 Causes of chick loss determined for Little Penguins breeding on Motuara Island and at Oamaru.
Figure 3.10  Chick growth curves for Little Penguins in Oamaru (solid black line - A-chicks, n = 57; dashed black line - B-chicks, n = 38) and Motuara Island (solid grey line - A-chicks, n = 17; dashed grey line - B-chicks, n = 7); detailed distributions of chick weights are given in Appendix III.
3.4 DISCUSSION

Device effects

Any alteration to the fine-tuned body shape of penguins inevitably has effects on their behaviour and capabilities (Bannasch et al. 1994, Bannasch 1995). When using external devices on penguins, hydrodynamic effects (additional drag) must be considered. Weavers et al. (1991) used VHF transmitters on Little Penguins in Australia. They estimated the additional drag caused by their devices to be up to 17% of the penguins' normal drag. The devices used in that study were slightly smaller than mine; as I had to be able to replace batteries in the field the increase in device dimensions was necessary. But in contrast to Weavers' study, I attached devices far on the lower back as suggested by Bannasch et al. (1994), which effectively reduces the drag from the transmitters.

A higher hydrodynamic drag may result in decreased swimming speeds as well as increased transport costs (Culik et al. 1994). As the probability of prey encounter may be directly related to the foraging range, penguins with transmitters probably have to increase their foraging effort to obtain the same amount of prey (Wilson & Culik 1992). Hence, using VHF transmitters on breeding penguins could influence chick growth and breeding success. In Oamaru, breeding success was lower in nests with equipped birds. However, this difference resulted from the fact that in transmitter nests, chicks hatched only from 67% of the eggs laid whereas the comparable figure in control nests was 87%. The actual survival rates of chicks did not differ. On Motuara Island, the breeding success in nests with equipped birds was actually higher than that in control nests.

Foraging ranges

Long-term trips

The stage of breeding is one of the main factors influencing the foraging ranges of penguins (e.g. Heath & Randall 1992, Weavers 1992). During the incubation phase Little Penguins in Oamaru and on Motuara Island generally made long-term trips. Only limited information is available about the duration of long-term trips made by birds from Oamaru. But it seems as if the penguins that travelled northwards along the coast did not return for more than six days, which is a comparable duration with long-term trips recorded for birds from Motuara Island (mean duration ~6 days). However, the data collection for incubating penguins at Oamaru took place during the early stages of the breeding season (3.7.-26.8.2000) and two of the three
monitored breeding birds on long-term trips abandoned their nest. Furthermore, Numata et al. (2000) found a significant difference in foraging trip durations for incubating Little Penguins at Oamaru and Motuara Island, with mean trip durations of three and six days respectively. Comparable results were apparent from my nest checks during the second sampling period at Oamaru (4.12.2000-21.1.2001). Therefore the long-term trips recorded at Oamaru may not necessarily be representative for the majority of incubating penguins.

The destination of long-term trips could often not be determined since most of the birds left the receiving ranges. Nevertheless differences between penguins from Oamaru and Motuara Island were obvious. Penguins from Oamaru travelled northwards on an inshore course in waters not deeper than 20 m. This corresponds well with findings for Little Penguins in Australia that travel mainly in shallow coastal waters, which probably is related to the distribution of their main prey species (Weavers 1992). In contrast, the penguins from Motuara Island travelled in substantially deeper waters (> 50 m) of the Cook Strait.

Because of the fragmented nature of long-term tracks the explanations for these differences can only be of speculative nature. The northward travels of Oamaru birds may be related to the great river systems north of Oamaru (e.g. Waitaki, Rangitata and Rakaia River) that export nutrients from inland areas to the sea and result in increased productivity in the coastal waters (Sommer 1998). Why penguins from Motuara Island chose an offshore course along the 100m depth contour is not clear. It is possible that submerged rocks along that contour support small scale upwelling which brings nutrient rich deep water to the surface (Bearman 1989). Upwelling plays an important role in foraging behaviour of Humboldt penguins (Culik et al. 2000) and seems likely to influence Little Penguins on long-term trips in Australia (P. Dann, pers. comm.). On the other hand these offshore courses may also represent straight line travelling towards the north-western boundary of the Marlborough Sounds where water masses out of Golden Bay meet those of Cook Strait, which may have a positive effect on productivity.

Another striking difference between both study sites was that two Motuara Island penguins were observed on long-term trips when they were rearing chicks; all penguins from Oamaru left only for one-day trips once the chicks had hatched. One of the Motuara Island birds returned after one night at sea to feed its chicks. The other penguin did not return to feed its chicks for six days. During this time the chicks had to rely solely on the other parent to supply food, which reduces the chances of survival considerably (Renner 1998).
Chapter 3: Foraging ranges and breeding success

The food demands of penguin chicks rise continually with age and the adults' foraging effort must increase (Culik 1994). Adult penguins extend their foraging trips and increase their foraging effort to match their chicks' demands (Boersma et al. 1990). This strategy is commonly observed in Little Penguins from Phillip Island, Australia, where adults go to sea for two or three days during the late chick rearing phase (A. Chiaradia, pers. comm.). On the other hand, if the body condition of the adult penguin is poor, it may need to invest primarily in its own well-being at the expense and growth of its offspring (Watanuki et al. 1993, Numata et al. 2000). This may account for the long foraging trip despite the risk of nest failure (Bost & Jouventin 1990).

One-day trips

After the chicks have hatched, the foraging ranges of penguins are greatly reduced since the adult birds have to feed their offspring regularly (Wilson 1995). Especially during the guard stage Little Penguins share their daily nest duties undertake mainly one-day trips (Stahel & Gales 1987, Weavers 1992, Numata et al. 2000).

At Oamaru all radio tagged birds returned to their nests within one day at sea during all stages of chick rearing. However, the foraging ranges of one-day trips varied considerably. One-day trips were either short-range, where the penguins stayed well within a 15 km range from their nest and travelled shorter travel distances (Fig. 3.3) or long-range, where the birds covered greater distances during the day and swam much further away from their nest sites (Fig. 3.4). Since there were no correlations between short-range or long-range trips and breeding stage, weather or individual preferences, it seems very likely that these different foraging patterns were mainly driven by prey distribution. The probability of prey encounters is proportional to the distance travelled (Wilson & Wilson 1990). Therefore, the foraging parameters (foraging radius, distance travelled) probably reflect the foraging success of individuals. The main prey taken by Little Penguins at Oamaru is slender sprat (Sprattus antipodum) that appears in large shoals in the upper water column and seems to be abundant all year along the Otago coast (Fraser 1999, M. McGregor, pers. comm.). The patchy distribution of slender sprat may account for one-day trips with different foraging ranges. Penguins that encounter a large patch of prey early in the day probably follow the movements of their prey and stay within a relatively small area. On the other hand, birds that do not encounter large shoals may have to compensate for lower foraging success by travelling further (see also Wilson & Wilson 1990, Weavers 1992, Radl & Culik 1999).
On Motuara Island, all recorded one-day trips were in close range to the penguins’ nest sites. Apparently the entrance to the Queen Charlotte Sound with its steep depth gradient is a natural boundary that penguins on one-day trips generally do not cross. All birds— with one exception— that crossed the 50m depth contour stayed away for at least 2 days. Most penguin positions recorded on one day trips were within a 40 km² area west to north-east of Motuara Island. No penguin was located east of Motuara Island and only on one occasion did a bird forage south before returning to the shallow waters west of the island. The topographical features of Queen Charlotte Sound, therefore, seem to restrict the penguins’ foraging range on one-day trips; if prey is scarce the penguins ultimately have to leave Queen Charlotte Sound which results in prolonged foraging trips. In comparison, Little Penguins at Oamaru do not face any restrictions in their foraging range, either by topographic or bathymetric features, so that one-day trips with foraging ranges of up to 30 km are not unusual (Fig. 3.11).

**Travelling speeds**

All speed values presented in this study are mean horizontal speeds that derived from the distance between two consecutive position fixes that were taken 10 or more minutes apart. The speeds values should therefore not be confused with absolute speeds since the vertical component of the penguins’ movements (diving) as well as any deviations from a straight course between the positions are not included. Weavers (1992) recorded mean travelling speeds for radio tagged Little Penguins in Australia (1.5 km/h on one-day trips, less than 1 km/h on long-term trips) that were substantially lower than speeds recorded during this study. This is probably a result of the longer intervals between consecutive fixes used in Weavers’ study (30 minutes and more). My results are comparable with speeds estimated for Little Penguins by Dann & Cullen (1989). Absolute speeds recorded with speed recorders on Little Penguins in Tasmania averaged 6.5 km/h (Bethge et al. 1997). Therefore, the speeds determined in this study are representative of those for Little Penguins.

I did not find apparent differences in travelling speeds between the two study sites. However, the differences between individuals on one-day or long-term trips were striking and underline the fact that the penguins may try to compensate lower foraging success by travelling greater distances which results in higher travelling speeds.
Breeding success

The breeding success of Little Penguins at Oamaru during the last 10 years is known to be one of the highest recorded for this species (Perriman & Steen 2000, D. Houston, pers. comm.). In contrast, conspecifics from Motuara Island showed low reproductive success during the previous studies (Renner 1998, Numata 2000). The low success rates at Motuara Island are apparently due to nest failure at different breeding stages. Renner (1998) observed high chick mortalities and suggested that this may have been related to a die-off of pilchard during his study. Numata (2000), on the other hand, reported high nest failures during the incubation phase as the main reason for poor reproductive success. During my study, the breeding success at Motuara Island was again much lower than at Oamaru. However, the comparison of breeding parameters reveals that hatching success at Oamaru was only marginally higher than on Motuara Island and may be explained with better breeding conditions at Oamaru due to nest boxes (Perrimen 1997, Renner 1998). Instead fledging success rates at both sites differed significantly and poorer breeding success on Motuara Island resulted, therefore, from higher chick mortality.

The main reason for fledging failure on Motuara Island was starvation; at Oamaru starvation was not an issue (Fig. 3.8). What is more striking is that most of the chick deaths on Motuara Island happened during two distinct periods (Fig. 3.12). The increased chick mortalities during the first period (2.10 – 7.10.) were mainly due to a spell of heavy rainfall that resulted in flooded burrows (chicks drowned, died of hypothermia). During the second period (26.10. - 11.11.) the chicks in all observed nests lost weight, in some cases dramatically, and a total of 22 chicks died of starvation. The reasons for this “starvation period” are unclear. A change in the weather occurred in early November resulting in much cooler air temperatures. However, mass gain of chicks started to decline a week before that. Therefore, it seems likely that a sudden variation in prey availability forced all adult penguins to undertake long-term trips. Unfortunately, no tracking data is available for that period. All chicks that survived after the 11.11. gained weight and most of them eventually fledged.
Conclusions

The breeding performance of Little Penguins varies greatly between years and between locations (Reilly & Cullen 1981, Cullen et al. 1992, Perriman & McKinlay 1995, Perrimen 1997). The main factor influencing these variations is likely to be the prey availability close to the breeding sites (Wilson 1995). The penguins at Oamaru can respond to low foraging success with increased foraging effort and extended foraging ranges. Apparently the prey abundance in the waters within one-day trip range of their nest sites is high enough to allow the birds to return to feed their chicks every night. In comparison, Little Penguins from Motuara Island have to leave Queen Charlotte Sound if foraging success within the Sound is insufficient. In this case the birds have to increase their foraging effort considerably and often do not return on the same day. The duration of these prolonged foraging trips during the chick rearing phase depend mainly on the foraging success of the individuals and may reflect their foraging qualities. However, it seems as if sudden time dependent changes in prey availability during this study resulted in low foraging success of all penguins and increased chick starvation; comparable observations were reported by Renner (1998). Overall it seems as if the population of Little Penguins has declined during the last years. Since there is a positive correlation between the chicks fledging mass and their survival during their first year (Dann 1988) it seems likely that the lower fledge masses recorded at Motuara Island may result in lower recruitment rates of Little Penguins.
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Figure 3.11 Comparison of foraging ranges of Little Penguins from Motuara Island (A) and Oamaru (B) on one-day trips. Areas within a 15 km Radius from the nest sites (black) are coloured dark grey, areas within a 30 km Radius light grey. Areas penguins generally did not reach during one-day trips are coloured white (areas beyond 30 km radius or with depths >50m). Note the different scales of both figures.
Figure 3.12  Dates of chick deaths on Motuara Island, Queen Charlotte Sound. Two periods of increased mortality can be distinguished: during the time of 2.10. - 7.10. heavy rainfalls flooded burrows, chicks died of drowning or hypothermia; during the period 26.10. - 11.11. chicks in all observed nests lost weight and 22 eventually died of starvation
3.5 REFERENCES


Chapter 3: Foraging ranges and breeding success


Chapter 4

Location dependent variations in diving behaviour of Little Penguins (*Eudyptula minor*) in New Zealand

4.1 INTRODUCTION

Penguins play an important role as top predators in the marine environment and have considerable impact on the food resources in their areas of distribution (Croxall 1984, Croxall & Davis 1999). As land-based breeders their foraging ranges are generally reduced during the breeding period (e.g. Heath & Randall 1989, Weavers 1992, Williams 1992, Hull 1997) with penguins relying on the availability of prey within close range of their nest sites. To overcome prey scarcity or low foraging success in those areas, penguins have to increase their foraging effort by extending their foraging trips and diving performance (Watanuki *et al.* 1993, Wilson 1995, Bethge *et al.* 1997, Numata *et al.* 2000).

Diving performance and behaviour have been studied in many penguin species using various data logging units (discussed by Wilson 1995). While diving behaviour of larger penguin species has been studied in great detail (e.g. King penguins, *Aptenodytes patagonicus*; Kooyman *et al.* 1992, Pütz 1994, Pütz *et al.* 1998), only a few comparable investigations have been conducted on the smallest of all penguins, the Little Penguin (*Eudyptula minor*) (Montague 1985, Gales *et al.* 1990, Bethge *et al.* 1997). All of these studies focussed on birds from one local population. However, studies on other penguin species showed that foraging and diving behaviour in a single species varies greatly with time (Watanuki *et al.* 1993) and in relation to environmental characteristics of the breeding locations (Croxall & Davis 1999, Radl & Culik 1999).

Little Penguins breeding on New Zealand’s South Island occupy habitats ranging from rocky shorelines along the east and west coasts, to the extensive water ways of the Marlborough Sounds and Fiordland in the northeast and southwest respectively. Comparative studies of two populations of Little Penguins on Motuara Island (41°06'S, 174°16'E) in Queen Charlotte Sound and at Oamaru (45°06’, 170°58'E) revealed large differences in foraging trip durations...
and breeding success (Numata et al. 2000) as well as foraging ranges and movements at sea (determined via VHF telemetry, see Chapter 3). According to these studies, the variations in at-sea behaviour seem to be related to environmental features at both sites. The range of Little Penguins from Motuara Island on one-day foraging trips is limited by geographical (topography of Queen Charlotte Sound) and bathymetrical features (sharp gradients from shallow waters to >100m depths); the total foraging area for one-day trips lies within a 9km radius from the island (Chapter 3). On the other hand, the foraging ranges of Little Penguins at Oamaru seem to be limited mainly by the birds’ physical capabilities and foraging radii of up to 30km² away from their nest sites were recorded.

These findings imply that there will be differences in diving behaviour between the two sites. Therefore, the aim of this study was to examine the differences in diving performance of Little Penguins breeding on Motuara Island and at Oamaru. The study based on the following predictions:

(i) The greater foraging ranges of Little Penguins at Oamaru are a result of increased horizontal movements; this should be reflected in a high proportion of shallow travelling dives and fewer dives into greater depths.

(ii) In contrast, Little Penguins from Motuara Island with their limited foraging ranges should spent considerably less time travelling which allows them to search greater volumes of the water column and, thus, dive deeper.

In this paper, I present the first comparative study of the diving behaviour displayed by Little Penguins that live and breed in different habitats. Using time-depth recorders (TDRs) I examined their dive performances and profiles.
4.2 MATERIALS AND METHODS

Dive data was collected during the 2000/2001 breeding season on Motuara Island (41°06'S, 174°16'E) in Queen Charlotte Sound between 6.9.2000 - 28.11.2000 and at Oamaru (45°06'S, 170°58'E) in Otago from 4.12.2000 - 21.1.2001. Further details on study areas are given in Chapter 2. Five adult Little Penguins on Motuara Island and six adult penguins at Oamaru were fitted with streamlined time-depth recorders (TDR). The devices were attached to the birds’ lower back (following Bannasch et al. 1994) with black adhesive tape (TESA tape, No. 4651, Baiersdorf AG, Hamburg, Germany; Wilson et al. 1997). The devices were removed after two to five days, so that one to three foraging trips were recorded for each bird. All equipped penguins were breeding birds with chicks. On Motuara Island I attached TDRs to adults only during the guard stage (the first 15 days after the chicks have hatched, Williams 1995), as recapturing adult penguins during post-guard of breeding proved to be problematic.

I used streamlined MK7 time-depth recorders (Wildlife Computers, Redmond, WA, USA) that weighed 32 g and measured 65 x 12 x 8 mm (L x W x H) with a frontal area (~144 mm²) that amounted to less than 2% of the penguins cross-sectional area. The TDRs recorded depth (through a pressure transducer, range: 0-100 m, resolution: 0.5 m), temperature and light level with respect to time. The TDRs were programmed to record depth in 1 s-intervals, temperature was stored every 2 seconds and light level every 10 seconds. The depth and temperature sensors were calibrated in the field using a commercial dive computer (depth resolution 0.25m) and an electronic thermometer (temperature resolution: 0.05°C). In calm conditions, the depth recorded by the devices was found to be accurate at depths >1 m. However, depending on sea conditions the pressure transducers could show strong fluctuations in depths <2 m so that the depth threshold for dive analysis was set to 2 m.

Recorded data was transferred to a notebook computer via serial interface and decoded to ASCII file format using the software HEXDEC (Ver. 1.00.09, Wildlife Computers). Analysis of the dive parameters was carried out in ANDIVE 8.0 (Jensen Software, Laboe, Germany), which assesses dive depth and calculates dive parameters such as total dive duration, duration of descent and ascent phases relative to the surface as well as maximum dive depth, bottom time and amplitude of U-shaped dives (as discussed by Wilson 1995).

Temperature data were used to determine the start and end of each foraging trip. Generally the temperature dropped sharply when the bird entered the water; we defined the onset of this
temperature drop as "start time" of the foraging trip. As long as the penguins' were at sea the recorded temperature fluctuated only marginally. The end of a foraging trip was indicated by a strong temperature increase; the onset of that temperature increase was considered as "end time" of the foraging trip.

Light data were used to get information about the light conditions at sea with respect to dive depths. The light sensors recorded light intensities in unspecified units. Light data were transformed into relative values for each foraging trip. This was achieved by determining the relative minimum and maximum of light intensity recorded by the TDR. To estimate the minimum I used the mean value of light readings that were recorded during the hours of darkness and obviously represented the light conditions in the penguins' nest; these periods were marked by low readings that did not vary over a longer period of time and changed only when the bird left its nest and/or daylight was present. The relative maximum of light intensity was estimated by using the mean value of all light readings recorded when the bird was at sea and at the surface (depth = 0 m). The difference of the mean maximum value (calculated separately for each foraging trip) and mean minimum value was defined as maximal daily light intensity. Light conditions in each depth class were estimated using the mean of light readings for each class minus the minimum value and are expressed as percentage of the maximal daily light intensity.

All data were analysed statistically using Minitab for Windows (Version 13, Minitab Inc., PA, USA) and WinSTAT for Microsoft Excel (Ver. 2000.1, R.K. Fitch, http://www.winstat.com). All means are presented ± 1 standard deviation. Comparisons between the study sites with respect to foraging and dive parameters were made using Student's t-test after testing for normality (Kolmogorov-Smirnov/Lillefors-test for normality). Furthermore, dive parameters were compared between both sites with respect to time of the day and depth using the non-parametric Wilcoxon test for paired comparisons.
4.3 RESULTS

On Motuara Island 8 foraging trips (<1 day) from 5 Little Penguins equipped with TDRs were recorded. At Oamaru a total of 10 one-day foraging trips were recorded from 6 individual penguins. All trips accounted for 9303 and 8066 diving events recorded at Motuara Island and Oamaru, respectively.

**Foraging trip durations**

Little Penguins from Motuara Island foraged for an average of 15.8 hours (S.D. = 0.4, range = 15.4 - 16.4, n = 5); in comparison birds from Oamaru made significantly longer foraging trips with an average of 17.0 hours (S.D. = 0.77, range = 16.2 - 18.0, n = 6; t-test: \( t_9 = -3.12, p < 0.05 \)). There was a strong correlation between trip durations recorded at both study sites and the hours of daylight during the sampling period, which averaged 13.4 hours (16.10.2000 – 26.10.2000) and 15.6 hours (6.12.2000 – 27.12.2000) for Motuara Island and Oamaru respectively (n = 18, \( r = 0.661, p < 0.005 \)). Little Penguins from Motuara Island generally went to sea 2.1 hours (S.D. = 0.34, range = 1.7 - 2.5, n = 5) before sunrise. Penguins from Oamaru left their colony between 1.6 hours (S.D. = 0.5, range = 0.8 - 2.2, n = 6) before sunrise, but this difference was not significant (t-test: \( t_9 = 2.04, p > 0.05 \)). Penguins generally returned to land 0.3 hours (S.D. = 0.2, range = 0.1 - 0.6, n = 5) hours and 0.4 hours (S.D. = 0.2, range = 0.1 - 0.7, n = 6) after sunset at Motuara Island and Oamaru, respectively (t-test: \( t_9 = -0.53, p > 0.05 \)).

**Dive frequency**

The diving behaviour of Little Penguins from Motuara Island and Oamaru differed markedly. The diving activity (time spent diving per total trip duration) of penguins from Motuara Island was more than double that recorded at Oamaru; the average number of dives made per hour by Oamaru birds was only two-thirds of that made by Motuara Island birds (Table 4.1). The difference between the sites was even more striking when the number of dives was considered with respect to hour of the day. Penguins from Motuara Island displayed an almost symmetrical distribution of dive frequencies over the course of the day. More dives occurred in the early hours of the day, the frequency then decreased towards a low around midday (12:00 to 14:00 hrs) and increased again until the end of the foraging trip (Fig. 4.1). In
contrast, penguins from Oamaru did not show an obvious pattern in dive frequency during the day and showed a significantly lower dive frequency in all hour classes (Wilcoxon test, $n = 16$, $Z = -2.50$, $p < 0.01$).

Given that penguins are visual feeders, Little Penguins from Motuara Island showed a surprisingly high dive frequency in the hours before sunrise, when no daylight was present (Fig. 4.1). At Oamaru the dive frequency was minimal before the first light (approx. 45 minutes before sunrise).

**Dive depths**

Little Penguins dived significantly deeper at Motuara Island (Table 4.1). The distribution of maximum depths for all recorded dives at both sites is given in Figure 4.2. Penguins from Motuara Island used a much larger vertical portion of the water column during their dives whereas penguins from Oamaru tended to stay in the upper 10 m. At Motuara Island, a change in diving depth during the day was apparent. In the early morning hours (4:00 to 10:00 hrs) only 26% of the recorded dives were deeper than 10 m. This changed during the middle of the day (10:00 to 15:00 hrs), where penguins dived deeper than 10 m on 61.6% of all dives. During late afternoon and towards evening (15:00hrs – 20:00 hrs) the dives were shallower again (only 33.6% deeper than 10 m). At Oamaru the majority of dives were in depth ranges from 2 to 10 m and the frequency of dives that were deeper than 10 m never exceeded 12% at any time during the day (4:00-10:00hrs – 9.2%, 10:00-15:00 hrs – 11.2%; 15:00-20:00 hrs – 8.3%). A comparison of mean depths reached by the birds with respect to one-hour-classes was significantly different between both sites (Wilcoxon test, $n = 16$, $Z = -3.36$, $p < 0.001$).

**Dive duration**

The mean dive durations of all recorded dives were significantly longer at Motuara Island (Table 4.1). Over the course of the day, the mean dive durations recorded for birds from Motuara Island increased during the morning and reached a distinct peak around midday (Fig. 4.3 – 36.1 seconds for the 13:00hrs class); after that, dive durations decreased again towards the evening. Dive durations observed for penguins from Oamaru also increased during the morning hours, but did not vary greatly in the middle of the day (Fig. 4.3). The penguins at Motuara Island made significantly longer dives in all hour classes (Wilcoxon test, $n = 16$, $Z = -
Chapter 4: Diving Behaviour

-3.52, p < 0.001). At Motuara, the dive durations increased significantly with dive frequency and depth, but no such correlations were found at Oamaru (Fig. 4.4 and Fig 4.5).

A different picture emerges if Motuara Island and Oamaru are compared using the dive durations in relation to different depth classes (Fig. 4.6). In all depth classes from 10 to 30 m penguins from Oamaru showed significantly longer dive durations than penguins from Motuara Island (Wilcoxon test, n = 5, Z = -2.02, p < 0.05). Hence, the overall longer dive durations determined at Motuara Island (Tab. 4.2) are mainly a result of the higher proportion of deeper dives (10 - 30 m).

Dive profiles

The dive profiles of Little Penguins for most part conformed to the V- and U-shaped categories of dives of Wilson (1995). When making V-dives the birds dived down to the maximum depth and returned either immediately or after a brief period (< 3 seconds) back to the surface. During U-dives the birds stayed more than 3 seconds at their maximum depth (bottom phase) before returning to the surface. U-dives are generally considered to be prey capture dives (Wilson 1995, Wilson et al. 1996, Radl & Culik 1999). However, the high proportion of U-shaped dives recorded at both Motuara Island (80.3%) and Oamaru (73.2%) suggests that Little Penguins also use U-shaped dives for prey searching. These dives varied with respect to the dive profile displayed during the bottom phase. On some dives, the birds did not move up or down and stayed at the same depth during the bottom phase. On other dives the birds seemed to be gradually ascending before making a steep and direct return to the surface. These two types of U-shaped dives probably represent searching behaviour. U-dives that may indicate active prey capturing had a bottom phase with sudden changes in depth so that the bottom period had an irregular W-shape (see also Radl & Culik 1999, Hull 2000).

The vertical distribution of depths reached during U-shaped dives is given in Figure 4.7. Birds at Oamaru primarily showed U-dives in the upper 12m whereas at Motuara Island the depths of such dives are more evenly distributed in depths between 9 and 20m.
Individual differences of diving behaviour within the colonies

To compare variations of diving behaviour within the colonies on Motuara Island and at Oamaru, hourly means of the dive parameters (number of dives, dive duration, max. depth, number of U-shaped dives) were used; only data from penguins the made at least 2 foraging trips were included. Values were only included when recorded during hours of daylight; all diving events before sunrise and after sunset were rejected. Diving parameters differed greatly between individuals at Motuara Island (Table 4.2). At Oamaru significant differences occurred only in dive durations and dive depths; number of dives did not differ significantly between individuals.
### Table 4.1 Comparison of foraging and diving parameters (individual means) of little penguins from Motuara Island and at Oamaru.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Motuara Island</th>
<th>Oamaru</th>
<th>$t$-test</th>
<th>$d_f$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>SD</td>
<td>Range</td>
<td>N</td>
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<tr>
<td><strong>Diving Behaviour</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diving activity (%)</td>
<td>5</td>
<td>61.3</td>
<td>4.9</td>
<td>52.9-65.1</td>
<td>6</td>
</tr>
<tr>
<td>Dives per trip</td>
<td>5</td>
<td>1165.3</td>
<td>136.5</td>
<td>960.0-1271.0</td>
<td>6</td>
</tr>
<tr>
<td>Dives per trip &amp; hour</td>
<td>5</td>
<td>75.3</td>
<td>10.5</td>
<td>60.5-88.1</td>
<td>6</td>
</tr>
<tr>
<td>U-dives per trip</td>
<td>5</td>
<td>914.6</td>
<td>79.5</td>
<td>837-1048</td>
<td>6</td>
</tr>
<tr>
<td>V-dives per trip</td>
<td>5</td>
<td>250.7</td>
<td>138.0</td>
<td>80.5-411.0</td>
<td>6</td>
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<td><strong>All dives</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. depth (m)</td>
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<td>10.1</td>
<td>5.6</td>
<td>2.5-35.5</td>
<td>8066</td>
</tr>
<tr>
<td>Duration (s)</td>
<td>9323</td>
<td>29.5</td>
<td>12.9</td>
<td>3-83</td>
<td>8066</td>
</tr>
<tr>
<td><strong>U-dives</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. depth (m)</td>
<td>7401</td>
<td>10.4</td>
<td>5.7</td>
<td>2.5-35.5</td>
<td>5903</td>
</tr>
<tr>
<td>Duration (s)</td>
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<td>32.4</td>
<td>12.1</td>
<td>6-83</td>
<td>5903</td>
</tr>
<tr>
<td>Bottom time (s)</td>
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<td>7.6</td>
<td>3-67</td>
<td>5903</td>
</tr>
<tr>
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<td>2.7</td>
<td>0-18</td>
<td>5903</td>
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<td><strong>V-dives</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. depth (m)</td>
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<td>5.1</td>
<td>2.5-22.5</td>
<td>2166</td>
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<tr>
<td>Duration (s)</td>
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<td>18.2</td>
<td>9.4</td>
<td>3-51</td>
<td>2163</td>
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</table>

*indicates no significant difference between study sites
### Table 4.2 Intracolonial comparison of individual dive parameters (hourly means) recorded for Little Penguins on Motuara Island and at Oamaru.

<table>
<thead>
<tr>
<th>Dive parameters (h⁻¹)</th>
<th>Motuara Island</th>
<th>Oamaru</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>median range</td>
<td>$H$</td>
</tr>
<tr>
<td>No. of dives</td>
<td>69 - 91</td>
<td>11.44</td>
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<td>Dive duration (s)</td>
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<tr>
<td>Max. depth (m)</td>
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<td>10.98</td>
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<tr>
<td>Dive duration (s)</td>
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<td>Max. depth (m)</td>
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<td>18.1</td>
</tr>
<tr>
<td>No. of U-dives</td>
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* indicates no significant difference between individuals
Figure 4.1 Average number of dives made (± standard error) by Little Penguins from Motuara Island (5 birds) and Oamaru (6 birds). Grey areas represent night and hatched areas represent sunrise and sunset.
Figure 4.2  Maximum depth of all dives made by Little Penguins from Motuara Island (n = 9370) and Oamaru (n = 8081) over the course of the day
Figure 4.3 Comparison of mean dive durations (± standard error) over the course of the day (1 hour classes) of Little Penguins from Motuara Island and Oamaru. All birds returned to land before 20:00hrs and 22:00hrs at Motuara Island and Oamaru, respectively.
Figure 4.4 Correlation of mean dive duration and number of dives for 1 hour classes. For Little Penguins from Motuara Island a strong correlation was obvious ($r = -0.873, p < 0.001$); in contrast there was no correlation at Oamaru ($r = 0.172, p > 0.05$). Note: dives made on the first and the last hour of the penguins’ foraging trips were excluded because only few dives were recorded and resulted in outlying values.
Figure 4.5 Correlation of mean dive duration and mean maximal depth reached for 1 hour classes. Little Penguins from Motuara Island dived significantly longer with increased depth ($r = 0.919$, $p < 0.001$). Only a weak correlation was found at Oamaru ($r = 0.375$, $p > 0.05$). Note: dives made on the first and the last hour of the penguins’ foraging trips were excluded because only few were dives recorded and resulted in outlying values.
Figure 4.6 Comparison of mean dive duration (± standard deviation) for different depth-classes between Little Penguins from Motuara Island (n = 9323) and Oamaru (n = 8081). Depth threshold was 2m. Note the lower dive durations recorded for birds from Motuara Island in depth classes >10m. The Aerobic Dive Limit (ADL) determined for Little Penguins by Bethge et al. (1997) lies between 42 and 50 seconds.
Chapter 4: Diving Behaviour

Figure 4.7 Frequency distribution of depths reached during U-shaped dives recorded for Little Penguins at Motuara Island and Oamaru. At Motuara Island 95% of all U-dives were recorded in depth ranges of 2-21m; at Oamaru 95% of all U-dives occurred in the upper 14m of the water column.
4.4 DISCUSSION

Externally attached devices alter the streamlined body shape of penguins and may affect penguins at sea (Wilson & Culik 1992, Bannasch et al. 1994, Bethge et al. 1997). The impact of the TDRs used in this study could not be assessed. However, in a previous study involving slightly larger devices on Little Penguins in Tasmania, it was found that the instruments did not significantly influence mean swimming speeds and increased the energy consumption only in certain speed classes (Bethge et al. 1997). Nevertheless, as negative impacts of externally attached devices cannot be completely ruled out, the results derived from such studies as this one may represent a merely conservative description of the penguins' diving behaviour (Bannasch 1995).

Diving behaviour with respect to time of day

The foraging trip durations displayed by Little Penguins at both study sites was related to the day-length. Overall, most diving activities took place during the hours of daylight. However, diving activities before sunrise indicated some differences between both populations. Penguins are mainly visual foragers and it seems unlikely that prey searching behaviour sets in before first light (Williams 1995). Shallow dives during hours of darkness have been observed in other penguin species and these are generally described as travelling dives (e.g. Pütz et al. 1998, Hull 2000). Comparable diving patterns have been reported for Little Penguins (Gales et al. 1990, Bethge et al. 1997). This is consistent with the results from Oamaru, where the frequency and depth of dives increased considerably with first light (approximately 30 minutes before sunrise). However, penguins from Motuara Island showed a number of deeper dives (5 to 10m) in the time before the first light. Considering the restricted foraging ranges (see Chapter 3) and the depths at which these pre-dawn dives occurred, it seems unlikely that these dive patterns represent only travelling behaviour. Instead, the dive profiles during this time suggest searching activities.

During the course of the day penguins from Motuara Island showed a strong correlation between dive duration and dive frequency (Fig. 4.4) as well as dive duration and depth (Fig. 4.5). The penguins tended to dive deeper and longer around midday, resulting in fewer dives. This underlined the relationship of diving behaviour and light intensity. Light penetrates to deeper depths when the sun reaches its zenith (Lalli & Parsons 1997, Sommer 1998). It seems
likely that the penguins use the higher light intensities at midday to hunt for prey in deeper waters and, therefore, extend the vertical component of their dives. Such relationship between dive depth and light intensity has been reported for several penguin species (e.g. Wilson et al. 1989, Wilson et al. 1993, Putz 1994, Radl & Culik 1999). On the other hand, the Little Penguins from Oamaru did not show any correlation between their dive patterns and the time of the day. The birds primarily foraged in the upper 10m of the water column at all times and only occasionally reached greater depths. A comparison of the light levels recorded by the TDRs at both study sites revealed that the average light conditions in the upper 14 m were better at Oamaru but light intensity showed a stronger decrease with depth than that found at Motuara Island (Fig. 4.8). Therefore, poor light conditions may have made deeper dives less favourable at Oamaru. It is possible that sediments transported by the Waitaki River (20 km north of Oamaru) cause some degree of turbidity of the coastal waters. However, it is also likely that the dive depth is strongly influenced by the vertical distribution of prey. The main prey species taken by Little Penguins at Oamaru is known to be slender sprat (Sprattus antipodum) that form large shoals in the surface regions of the water column and are abundant all year (Fraser 1999). No detailed information on the main prey is available for Little Penguins from Motuara Island.

Diving behaviour with respect to dive depth

The overall dive durations recorded at Motuara Island were significantly longer than those recorded at Oamaru. This difference resulted from the fact that Little Penguins from Motuara Island made a much higher proportion of deeper and, thus, longer dives than Little Penguins from Oamaru. If the diving behaviour is examined with respect to depths reached, it becomes clear that dive durations are comparable for depths <10 m, but that birds from Oamaru in fact dived significantly longer at depths >10 m (Fig. 4.6).

In swim canal and field experiments, Bethge et al. (1997) determined the Aerobic Dive Limit (ADL) of Little Penguins to be in the ranges of 42 to 50 seconds. Any dive that is longer than the ADL requires anaerobic metabolism and longer recovery (resting) phases at the surface, which in turn reduces the time that the birds may spend under water searching for prey (Schmidt-Nielsen 1990, Kooyman & Ponganis 1994). Penguins and other seabirds rarely dive longer than their oxygen stores permit (e.g. Baldwin 1988, Kooyman et al. 1992, Bethge et al. 1997). Therefore, it seems reasonable to assume that if the animals extend dives beyond their
aerobic capabilities this happens for good reasons, e.g. feeding rather than searching. At Motuara Island most of the dive durations down to the 22 - 26 m depth class lay within the determined ADL and only on dives deeper than 26 m did the birds reach durations that exceeded the ADL (see Fig. 4.6). However, only few dives >26 m (0.4% of all recorded dives) were observed at Motuara Island. At Oamaru Little Penguins that dived deeper than 10m generally showed dive durations close to the ADL; dives deeper than 14m were longer than 50 seconds. Thus, most dives into depths >14 m (4% of all recorded dives) utilized anaerobic metabolism, which would have resulted in longer recovery phases at the surface. Furthermore, penguins that dived deeper than 14m did so on a number of consecutive dives ("dive bout") indicating a period of heavy feeding activity before taking a longer resting phase at the surface (Fig. 4.9). Overall, it seems as if the penguins from Motuara Island show prey searching behaviour in all depth classes <26 m, whereas penguins from Oamaru rarely search for prey in depths >14 m and only enter greater depths during active prey pursuit. Unfortunately, due to the fluctuations of the depth sensors in depths <2 m, it was impossible to determine precisely the duration of surface phases and, therefore, to analyze recovery times after deeper dives or dive bouts.

**Individual differences**

At both sites great variations in diving behaviour between individuals were apparent, which suggests that the penguins diving behaviour is not fixed within the population. These differences are not surprising since the main factors influencing the diving activities are the birds’ individual abilities and strategies as well as the varying distribution and patchiness of prey (e.g. Wilson *et al.* 1991, Kirkwood & Robertson 1997, Hull 2000). Another factor that may play a role in differences between individuals is body mass (Schmidt-Nielsen 1991). However, no information on body mass was obtained during this study.

It may seem surprising that the number of dives determined for individual penguins at Oamaru did not differ significantly (Table 4.2), especially given that single penguins at Oamaru showed remarkably different foraging behaviour on separate foraging trips. In two cases, birds showed high dive activity of up to 1400 dives per day on one foraging trip, but did not make more than 500 dives per day on the next foraging trip (2 days later).

With respect to the different foraging ranges displayed by Oamaru penguins (Chapter 3), these different diving patterns may represent short-range foraging trips, on which the birds do
not travel far away from their colony and spend more time diving (high dive activity), and long-ranged foraging trips, on which the birds travel considerable distances throughout the day and presumably feed primarily during dive bouts (low dive activity – see Figure 4.8). In the latter case, travel dives presumably occur near the surface at depths above the diving threshold, so that only feeding dives are recorded.

**Conclusions**

Little Penguins from Motuara Island and Oamaru show great differences in diving behaviour. These differences seem to be determined first and foremost by environmental features (coastal topography and bathymetry) of the different habitats the penguins occupy. Little Penguins from Oamaru tend to travel far greater distances which should increase the probability of prey encounters (Wilson & Wilson 1990). The birds increase their foraging efforts horizontally; foraging dives occur infrequently in distinct dive bouts. As predicted, this foraging behaviour is reflected in the diving performance with fewer and shallower dives than recorded at Motuara Island.

At Motuara Island, the foraging ranges of Little Penguins are largely limited by geographical features (landmasses) and the deep waters of Cook Strait. Therefore, the birds extend their foraging efforts primarily vertically and search the whole water column. The penguins generally dive deeper and maximum depths of the dives are widely distributed between the surface and the average depth of the outer Queen Charlotte Sound (15 – 30 m – see Fig. 4.2).

Little Penguins at Oamaru profit from the high and constant abundance of slender sprat and seem to feed almost exclusively on this species (Fraser 1999). There is no detailed information on the productivity and prey abundance in Queen Charlotte Sound. But the diving behaviour suggests that Little Penguins from Motuara Island must make greater efforts to obtain enough food and probably show a more generalized prey spectrum.
Figure 4.8 Light intensities for different depth classes (as percentage of mean surface value) determined from all light readings at sea. In the upper 10 m the light intensities are generally higher at Oamaru what could be explained with the time of year (longer days, longer sun path and therefore stronger radiation). But in comparison to light intensities recorded at Motuara Island, the light intensity shows a steeper decrease with increasing depth.
Figure 4.9  Dive bout of a Little Penguin from Oamaru, recorded during a one-day long foraging trip, displayed with ANDIVE 8.0. Upper graph: profile of the diving activities that occurred between 07:40 (left end) and 11:55 (right end). Lower graph: detailed sequence of dives that occurred between 10:40 and 10:50 (sequence marked in upper graph by a grey bar). The penguin started this sequence with 2 V-shaped dives that were followed by a series of W-shaped dives that probably represent feeding dives; dive durations are given above each dive. All dives deeper than 14m are longer than the Aerobic Dive Limit (ADL) determined for Little Penguins of 42 to 50 seconds (Bethge et al. 1997). The resting phase at the surface after this dive bout amounted to more than 4 minutes.
4.5 REFERENCES


Chapter 5

Conclusion

Little Penguins breeding at Oamaru and Motuara Island exhibit major differences in foraging behaviour and, as a consequence, breeding success. During the breeding season, the main function of the penguins' movements at sea is to obtain food for the offspring. Therefore, it is reasonable to conclude that behavioural differences observed at both sites are primarily influenced by local prey availability and distribution. Penguins feed mainly on mobile prey species (fish, squid), which do not occur in a defined space and require considerable searching effort and, thus, flexibility in foraging behaviour (e.g. Williams et al. 1992, Hull 2000). If the search for prey is unsuccessful within close range of the colony, penguins face basically two options to increase their foraging success. They can travel greater distances, which theoretically should increase the amount of prey encountered or, alternatively, increase their diving performance and search larger volumes of the water column (Wilson & Wilson 1990).

Taking into account the different habitats, it seems that penguins breeding on Motuara Island are at a great disadvantage compared to conspecifics at Oamaru: the foraging area is limited by the geographic features of the Queen Charlotte Sound and the waters of Cook Strait that represent a natural boundary to the Sound. The Strait's strong currents would not only require higher travelling effort by the penguins, but also may influence the distribution on prey considerably. The distribution of fish in deeper waters is often affected by bathymetrical features like rocks or islands that may create local upwelling, which in turn results in higher productivity around these areas (Bearman 1989, Lalli & Parsons 1997, Sommer 1998). The effort the penguins have to make to reach rocks and islands in Cook Strait is probably too great to make them suitable destinations for one-day foraging trips. Therefore, trips into Cook Strait are likely to result in long-term foraging trips (two days or longer). With respect to one-day trips, penguins from Motuara Island have only one choice to enhance their foraging success – to increase dive activity and search greater volumes of the water column within the outer Queen Charlotte Sound (Chapter 3).
At Oamaru, on the other hand, penguins face foraging areas that are only limited by the birds’ individual physical capabilities. If a penguin encounters a good patch of prey in relatively close vicinity to its colony, it increases its diving activity, presumably while following the movements of its prey (Chapter 4). Otherwise, the penguin must extend its foraging range and travel greater distances during the day (Chapter 3). These foraging tactics seems to be successful, allowing Oamaru penguins to return every night to feed their chicks which ensures strong chick growth, subsequently increases the survival chance of the offspring and results in the high breeding success rates reported from Oamaru (Perrimen & Steen 2000, D. Houston, pers. comm.).

By contrast, Little Penguins on Motuara Island have exhibited low breeding success rates during recent years. Prolonged foraging trips as a result of low prey availability were suggested as the main reason for nest failures and low breeding success (Renner 1998, Numata 2000). The findings of this study support these suggestions. However, it seems as if this is only one half of the explanation, because long-term trips during the later stages of the chick rearing phase are not unusual and do not necessarily have a negative effect on chick survival (Reilly & Cullen 1981, Stahel & Gales 1987, A. Chiaradia, pers. comm.).

The synchronicity of chick mortalities recorded during this study on Motuara Island, suggests that a temporary change of prey availability close to the island reduced the foraging success of all breeding pairs. During a two week period (‘starvation phase’), all chicks lost weight. Before this phase, chick growth was stable and comparable to that at Oamaru. After the starvation phase, the surviving chicks gained weight again and eventually fledged. It seems as if some event affected the foraging success of the adult penguins on one-day trips and forced them to undertake longer foraging trips that presumably led them into Cook Strait. Renner (1998) reported a mass pilchard die-off in 1995 and concluded that this event might have had negative effects on the breeding success determined on Motuara Island during this and the following year. No such event occurred during this study and the cause of the starvation phase is a mystery.
REFERENCES


Appendix I

VHF-Telemetry - Techniques

1.1 INTRODUCTION

With the advances in technology over the last two decades the methods for studying at-sea-behaviour of marine animals like penguins improved greatly. Various telemetric methods can be used to get information on many aspects of the animals' behaviour. Satellite-telemetry, VHF-telemetry and Geolocation (GLS) can be used to determine the positions of single animals during foraging trips, external data loggers can be deployed to record dive depths, temperature, swimming velocities and internal data loggers record ingestion rates and provide data on feeding frequencies (e.g. Weavers 1992, Wilson et al. 1994, Radl & Culik 1999, Culik et al. 2000).

However, to determine foraging ranges of Little Penguins there is currently no alternative method to VHF-telemetry. Satellite telemetry is mainly restricted by variable satellite coverage, resulting in too few position fixes each day to reconstruct single day foraging trips. GPS-loggers that determine travel routes through stationary satellites are slow to get position fixes and memory requirements of these loggers is too high to provide accurate tracking of marine animals (R.P. Wilson, pers. comm.). Dead reckoning devices that allow to determine travel routes through vectorial combination of directional data (recorded with a 3d-compass) and speed data are inaccurate in areas of strong currents ('drift effect' – Wilson & Wilson 1988; Wilson et al. 1991). Furthermore, most of the data logging devices are still too voluminous and not suitable for use on small animals like Little Penguins (Bannasch et al. 1994).

For this study two different methods were employed. To examine foraging ranges and travel routes VHF-telemetry was used involving the attachment of VHF-transmitters on Little Penguins that were then tracked by two land-based receiving aerials. The transmitter packages were specially constructed for this study. To determine diving behaviour, commercial time-depth recorders (TDRs – MK7 Wildlife Computers) were deployed that recorded dive depth, temperature and light level at free adjustable sampling intervals.
I.2 CONSTRUCTION OF VHF-TRANSMITTER PACKAGES

I developed a 30-gramm VHF-transmitter package that would be attached to the dorsal feathers. The design of the package had to fulfil certain prerequisites: low hydrodynamic drag (Bannasch et al. 1994); unobtrusive colouring to avoid attention of predators, prey and conspecifics (Wilson & Wilson 1988; Wilson et al. 1990); low mass/light weighted; shock resistant and waterproof; long lived and exchangeable batteries.

The core of the transmitter package was a MiPs-1B transmitter (Fig. I.1 – Reimesch Kommunikationssysteme GmbH, Auf der Kaule 23, 51427 Berg. Gladbach, Germany). The sizes of the transmitter core were – length: 15mm; width: 8mm; height: 2mm. For duty control a Reed switch was implemented in the power circuit so that the transmitter could be switched off by placing a magnet above the Reed switch. A total of 12 MiPs were available for this project. Every single transmitter core was set to a specific transmitting frequency that lay within a VHF-frequency band of 148 to 150 MHz. The pulse rate of the transmitter cores averaged between 60 and 80 pulses per minute but varied with battery conditions (Voltage, dampness). According to the manufacturer the maximum range of the MiPs-1B should be estimated to be between 40 and 50 Km.

Figure I.1 MiPs-1B transmitter core
The power supply for the transmitter core was provided through a cylindrical Lithium-battery (length: 18mm, diameter: 11mm). As battery compartment I used the lower ends of plastic test tubes (length: 25mm, diameter: 16mm). The battery compartment was installed in line with the transmitter core and resulted in an elongated transmitter package. My transmitter packages were longer than devices described by Weavers et al. (1991). However, in terms of hydrodynamic effects the length of an external device has no considerable effects (Bannasch et al. 1994). The battery compartment was sealed with silicon to avoid penetration of the polyester resin that was later used to finalize the transmitter package. To replace the battery in the field, the transmitter package was drilled open at its rear end; it was then possible to pull the battery out of the compartment and detach it from the cables leading to the sealed transmitter core. By choosing this transmitter design it was possible to replace faulty or exhausted batteries in the field without the need to reshape the transmitter pack.

For aerials I used stainless steel braid (length: 23cm, diameter: 2mm) that is used as rigging material of boats. Weavers et al. (1991) used fishing tackle with a 1mm diameter; I was unable to find a comparable material that had a satisfactory flexibility. The braid was light and bendable, so that theoretically slow swimming speeds of submerged penguins would be sufficient to bend the aerial into a horizontal position which greatly reduces the drag resulting from the aerial (J. Hennicke, pers. comm.). On the other hand, the strength of the braid was sufficient to bring the aerial into an upright position as soon as the penguin surfaced. For construction reasons the aerial was initially set perpendicular to the transmitter package. After moulding the transmitter casing with polyester resin (see below) the aerial was finally bent 60 to 70° towards the rear end of the device.

To finalize the transmitter casing, I designed prototypes from balsa wood. The shape of the prototypes followed the suggestions made by Bannasch et al. (1994). After fine shaping the prototypes were used to produce silicon moulds. The transmitter core and battery compartment were placed within the moulds and sealed with commercial polyester resin (Glosscoat polyester resin, Voss Chemie, Germany). After the resin had hardened the transmitter packages were sanded to their final shape. The dimensions of the finalized transmitter package were – length: 60mm, width: 20mm, height: 18mm (Fig. 1.2). The device weighed 35 grams. Of all 12 MiPs transmitter cores one was destroyed during the construction and two others malfunctioned in the field so that a total of nine transmitter packages could be used on penguins.
Figure 1.2  The finalized transmitter package
(aerial is not shown in complete length)
I.3 ATTACHMENT OF DEVICES

The devices used in this study (VHF-transmitter packages and TDRs) were both attached to the penguins' lower back using the 'Tesa-Tape-Technique', which involves adhesive cloth tape (Tesa-Tape No. 4651, Baiersdorf AG, Hamburg, Germany) to attach devices to the feathers (Wilson & Wilson 1989, Wilson et al. 1997). The technique worked perfectly for the elongated TDRs. However, I encountered some problems with the transmitter packages because of their small dimensions. To determine the best arrangement of tape stripes I conducted dummy tests on penguins at Oamaru before the breeding season started. During these tests, dummy transmitters (packages of solid polyester resin without electronics and aerial) were attached to penguins with different sized tape stripes (width, length) and the condition and durability of the dummy devices was controlled over the following days.

Using normal sized tape stripes (width: 18mm, length 50-100mm) proved inappropriate. The penguins at Oamaru land in extreme conditions (heavy surf), which causes great strain on the attached devices. Especially the slimmer front end of the devices tended to be ripped from the penguins' backs. Wide stripes had the disadvantage of binding fewer feathers because rows of feathers lay on top of each other rather than on the adhesive surface. This problem was solved using thinner stripes (width: 9mm). Eventually, a technique involving four thin stripes at the front and two wider stripes at the rear of the transmitter package was found to be a satisfactory attachment method (Fig. I.3). Only black coloured tape was used to keep the devices unobtrusive (Wilson & Wilson 1988, Wilson et al. 1990).

Figure I.3  Little Penguin equipped with transmitter package
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Figure I.3  Little Penguin equipped with transmitter package
I.4 IMPACT OF ATTACHED DEVICES ON PENGUINS

Penguins have a streamlined body that has the lowest hydrodynamic drag known in nature and engineering (Bannasch 1995a, Bannasch 1995b). By attaching external devices on penguins, the birds have to invest more energy when at sea. A main aim in the design of external devices is to find a shape that imposes the lowest additional drag. Bannasch et al. (1994) recommend attaching external devices as far down on the lower back on a penguin as the device dimensions permit. At this caudal position the device-induced turbulence – and, therefore, drag – is greatly minimized. However, Bannasch’s study focused mainly on recording devices (data loggers). Using VHF-transmitters the aerials cause additional drag that will exceed the drag of devices without an aerial (J. Hennicke, pers. comm.).

Weavers et al. (1991) estimated the additional drag of VHF-transmitters used on Little Penguins on Phillip Island, Australia, to be a maximum of 17% of a penguin’s usual hydrodynamic drag. Apparently Weavers’ transmitters were shorter and flatter than the devices used in this study (the actual dimensions of Weavers’ transmitters were not published); the length of the aerials (22 cm) only marginally longer and the aerials’ diameter was 50% (1mm) thinner than the aerials on my transmitters.

In Weavers’ study, the devices were attached to the penguins’ central back. According to Bannasch et al. (1994) this position causes strong turbulence and, therefore, high hydrodynamic drag. In this study, the transmitters were attached at the lower back, just above the penguins’ preen gland, which supposedly causes much less drag (Bannasch et al. 1994). Therefore, the additional drag of my devices was probably less or comparable with those values stated by Weavers. The more hydrodynamic shape of my devices would also have helped in lowering drag.

In the field, chick weights and breeding success of equipped penguins and control birds were used to get an indication of negative effects of devices on the penguins’ foraging behaviour.
1.5 RECEPTION OF TRANSMITTER SIGNALS

Setup of the Receiving stations

To track penguins equipped with transmitter packages, two land-based receiving stations were established. VHF signals from the transmitters were received through two antenna arrays. Each of these arrays comprised of two directional antennae (5-element Yagis, RA-NS, Telonics, AZ, USA) that were configured as a "Null Peak System". At each receiving station, two Yagi antennas were mounted parallel, 2.5 m apart from each other, to a horizontal mast. The horizontal mast was installed on a 3 m vertical pole which ran centrally through a round camping table and was fixed with ropes at about 2m. The base of the pole was fixed in a Teflon socket that allowed easy rotation of the antenna installation. Just above the table two handles were attached to the vertical pole. To record bearings a compass rose was fixed on the table and readings were taken using a pointer which was screwed to the pole just above the compass rose.

The "Null Peak System" is commonly used to get accurate bearings of a signal. The parallel Yagi antennae separately pick up the signal and pass it on as separate impulses to a modulator ("Null Peak Box"). The main purpose of this modulator is to merge the separate impulses back to a single signal, which is unperceivable when the signal is picked up by both Yagi antennae with equal strength. This is only the case when both Yagis are pointing directly towards the signal’s (the penguin’s) position.

The antenna arrays operated in the 148-150 MHz frequency band. The incoming signals received by the two Yagis ran through coaxial cables into the Null Peak Box and after modulation were delivered through a single coaxial cable to a Yaesu VHF-transceiver (Yaesu FT-290 RII – Yaesu Musen Co. Ltd. Japan). The transceiver could quickly be adjusted to all of the transmitters' specific frequencies. If the signal was weak, a pre-amplifier (ULNPA 150 with noise reduction, Reimesch Kommunikationssysteme GmbH, Germany) was connected between Null Peak Box and transceiver. Power supply at each receiving station was provided by means of a car battery that was permanently recharged through a solar panel.
Positioning of receiving stations

Positions of equipped penguins were calculated by triangulation of bearings recorded at each station within a timeframe of 10 minutes. To reduce the error of bearings it is necessary to position the receiving stations at a distance that the penguins' foraging area is covered equally by both antennae; in the optimal case the penguins would stay between both stations (see Zimmerman & Powell 1995). To increase the receiving range, the stations had to be placed at the highest elevation possible (on hills, high cliffs etc.). Elevation and geographical position of each station were determined to the nearest 10m using a GPS receiver (Garmin GPSII Plus). The constellations of the receiving stations in both study areas are given below.

Oamaru

The coastline around Oamaru runs more or less in a line northeast, which theoretically should provide good VHF coverage. However, a lack of points with reasonable elevation reduced the range of reception. Receiving station 1 ('Gun' - 45°06.73S, 170°58.94E, elevation: 61 m) was established not far from the Quarry nest area on a disused historic gun emplacement at one of the highest points around Oamaru. Receiving station 2 ('Dead Shark Beach' - 45°01.86S, 171°04.11E, elevation: 23 m) was located a few kilometre north of Oamaru on a cliff edge (Fig. I.4). The baseline (linear distance) between both stations was 11.7 km.

Motuara Island

The positioning of the receiving stations was primarily determined by the logistic difficulties associated with the isolated location of the study area. Receiving station 1 was established on the observation tower at the highest point on Motuara Island ('Motuara' - 41°05.74S, 174°16.43E, elevation: 148 m). Receiving station 2 was located on farmland Arapawa Island on the eastern side of Queen Charlotte Sound ('Arapawa' - 41°06.75, 174°22.20E, elevation: 426 m). The baseline was 7.9 km (Fig. I.4).
Figure 1.4  Position of receiving stations and distribution of reception qualities in both study areas:
A – Motuara Island, B – Oamaru, Δ - Receiving stations (see text for details)
Receiving ranges and reception quality

During test runs on land, the average range the transmitters was approximately 30 km. However, at sea the range should be better because of the absence of obstacles such as trees, buildings, and power lines that have negative effects on overland transmissions. Therefore the maximum range for the transmitter estimated by the manufacturer (40-50 km) seems reasonable. To estimate the actual at-sea-ranges of the devices, I calculated for each receiving station the distance to the horizon (optimal reception – Tab. I.1). Because of the curve of the earth this distance varies with the elevation of the antenna positions. The area of the sea that lay within the optimal coverage of both stations was termed ‘area of optimal reception’ (Fig. I.4). If the signal leaves the ‘area of optimal reception’ it does not disappear necessarily but will be considerably weakened (‘area of reduced reception’).

Table I.1  Theoretical reception radius in both study areas

<table>
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<th>Oamaru</th>
<th>Motuara Island</th>
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<td>Elev. [m]</td>
<td></td>
<td></td>
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<tr>
<td>Gun</td>
<td>61</td>
<td>148</td>
</tr>
<tr>
<td>Dead Shark Beach</td>
<td>26</td>
<td>47.7</td>
</tr>
<tr>
<td>Motuara Island</td>
<td>148</td>
<td>47.7</td>
</tr>
<tr>
<td>Arapawa Island</td>
<td>426</td>
<td>81.0</td>
</tr>
</tbody>
</table>

Distances of antenna - Horizon [km]*:  
- Oamaru: 30.6, 18.8  
- Motuara Island: 47.7  
- Arapawa Island: 81.0

* Calculated by $1.17 \times \sqrt{h} = D_{\text{Dist}}$ with $h =$ Elevation of aerial in feet, $D_{\text{Dist}} =$ Distance to horizon in nautical Miles  
(Nautical Know How Inc. - http://www.boatsafe.com/nauticalknowhow/distance.htm)

According to these results the radius of optimal reception in Oamaru is mainly restricted by the distance of antenna to horizon at ‘Dead Shark Beach’. However, on Motuara Island the distances of antenna to horizon at both stations lay beyond the transmitters’ maximum range which was therefore considered the limiting factor for the radius optimal reception.

Further limitations of signal reception

Apart from the radius of optimal reception, topographic characteristics of the study areas played an important role for signal reception. Hills, bays, coves, and islands can reduce or affect the signal quality. Consequently there can be areas where only one of the receiving stations can receive the signal, which is blocked by an obstacle from the other (‘area of one-sided reception’) as well as areas where none of the stations can receive the signal (radio shadow – ‘no reception’). In Oamaru such influences were greatly reduced by the lack of topographic obstacles (Fig. I.4). In contrast, the topography of the Queen Charlotte Sound
Appendix I: VHF telemetry - Techniques

around Motuara Island is marked by many bays, coves and islands and is flanked by high hill formations. However, during initial tracking tests with a transmitter on a boat I determined that the islands close to Motuara Island did not result in considerable radio shadow within the central areas of the outer Queen Charlotte Sound. Limitations of reception occurred when the transmitter was moved further into the Sound or left the Sound around Cape Jackson or Cape Koamaru. Another problematic area was the shallow stretch of water between Motuara Island, Ship Cove and Cannibal Cove (Fig. 2.1). In that area, the signals were probably reflected by the hill formations on the mainland, so that it was difficult to determine the Null Peak and therefore get an accurate bearing (Fig. I.4).

Shortwave signals cannot penetrate sea water. Hence, a transmitter’s signal cannot be received if the aerial is submerged – which happens when the penguin dives. Little Penguins show periods of concentrated diving behaviour where they often spend less than 10 seconds at the surface before the next dive (Weavers et al. 1991, Bethge et al. 1997). During these periods it is difficult to get an acceptable bearing on the signal and this can only be achieved by experienced operators.

Calibration of the compass rose

The data collected during VHF-telemetry consists basically of bearings recorded as degree values (azimuth) that are read from the compass rose at the base of the antenna. For a first basic calibration, the compass rose was set towards the magnetic north using a compass under consideration of local magnetic anomalies. However, the setup of the compass rose had to be checked regularly because either pointer or compass rose (which was fixed to the table) could be shifted accidentally by the operators. Furthermore, bearings taken on a signal are also affected by weather conditions (humidity, air pressure) and vary within an estimated range of 1 to 3 degrees (J. Hennicke, pers. comm.).

To record bearings independently from the setup of the compass rose or the pointer, I installed reference transmitters at certain point in both study areas. The exact positions of these reference points were determined with a GPS-receiver (Garmin GPSII Plus). From the coordinates of each receiving station and the reference point the ‘real’ azimuths between each station could be calculated. During the data collection, the operators of each station had to record a bearing of the reference transmitter hourly. From the difference of recorded bearing
and real azimuth it was possible to correct all bearings taken during the next hour. The operators did not know the exact value of the real azimuth to avoid “habitual bearings”.

**Estimation of operator errors and location errors**

All operators were introduced to the system and were trained to find correct Null Peaks – the bearing at which the signal cannot be perceived and the antenna is in line with the signal’s position. During these training sessions, every operator had to record bearings on signals that were positioned on certain land based locations with known coordinates so that the real azimuth could be determined. The difference of real bearings and those recorded by the operators was used to calculate the ‘average azimuth error’. This error generally lay between 0 and 1.5°. Weather effects were ruled out since all training sessions were conducted in good weather conditions.

The precision of position fixes calculated from two bearings varies with bearing errors at each station (Weavers et al. 1991). The deviations between recorded and real azimuth (average azimuth error) result in a four sided “error polygon” (for two receiving stations – Fig. 1.5). The area covered by that polygon indicates the accuracy of a calculated position fix. The size and dimension of the error polygon depends on the signals’ position. This polygon gets bigger with increasing distance between signal and receiving stations; if the signal moves out of the area between both stations, the polygon elongates (Fig. 1.5). The size of the error polygon can be minimized by increasing the length of the baseline linking the receiving stations (Zimmerman & Powell 1995).

![Figure 1.5](image.png)
To estimate the location error of a position fix in relation to the signals’ position, the theoretical length of one side of the polygon resulting from the average azimuth error was calculated. For that purpose the GPS- and Mapping Software “GPS Trackmaker Version #11” (O. Ferreira, Belo Horizonte, MG, Brazil – http://www.gpstm.com) was used to calculate the polygon dimensions with a precision of ± 100m. Tables I.2 and I.3 show the ‘maximum location error’ for both study areas with the signals’ position being at three different distances (10, 20 and 30 Km) and two different angles from the centre point of the baseline (see Fig. 1.5).

| Table I.2 Maximal location error* – Oamaru; avg. azimuth error: 1.5°; baseline: 11.7 km |
|----------------------------------------|------------------|------------------|------------------|------------------|
| Distance [km]                         | 90°              | 30°              | 90°              | 30°              |
| 10                                    | 0.4              | 0.6              | 0.4              | 0.6              |
| 20                                    | 1.3              | 1.9              | 1.3              | 1.9              |
| 30                                    | 2.4              | 3.6              | 2.4              | 3.6              |

* for 2 receiving stations (Null Peak configuration)

The considerable distance (baseline) between both receiving stations at Oamaru induced a reduced error polygon. However, initial results showed that a great percentage of the penguins’ positions were between 15 and 25 km therefore mainly in an area with bigger location errors (error polygon is larger).

| Table I.3 Maximal location error* – Motuara Island; avg. azimuth error: 1.5°; baseline: 7.9 km |
|----------------------------------------|------------------|------------------|------------------|------------------|
| Distance [km]                         | 90°              | 30°              | 90°              | 30°              |
| 10                                    | 0.6              | 0.7              | 0.6              | 0.7              |
| 20                                    | 2.3              | 2.6              | 2.3              | 2.6              |
| 30                                    | 3.8              | 5.0              | 3.8              | 5.0              |

* for 2 receiving stations (Null Peak configuration)

The shorter baseline at Motuara Island resulted in a larger overall location error. But Little Penguins in that area stayed generally in a closer range and most positions lay, therefore, in an area with less influence of azimuth errors (error polygon is smaller).
1.6 DATA COLLECTION AND ANALYSIS

Recording telemetry data in the field

Penguins were generally tracked from sunrise to sunset. However, on a number of days the fieldwork had to be started later or called off earlier due to unsuitable weather conditions. Depending on the numbers of birds at sea the intervals at which bearings were taken on individual penguins, was either 10 or 15 minutes.

To get information on all aspects of the signal received and to make it easier to record tracking data I compiled data sheets (see Appendix II). A description of the different parameters that were recorded is given below.

Null width

The “Null peak” (i.e. the bearing at which the signals could not be perceived) seldom lies at one certain azimuth value. Usually the range of a Null peak covers two or more degrees on the compass rose. In this case, the median value of this range was considered as the correct bearing (‘Azimuth’). To estimate the quality of a recorded bearing, three different classes of ‘Null width’ (range of the Null peak) were described. Null widths < 3° were considered as optimal Null peak. Null widths in the range of 3 to 12° were considered as acceptable Null peak. Null widths >12° were considered as poor Null peak.

Signal quality

Little Penguins show different phases of diving behaviour over the course of the day which result in different patterns of transmission breaks (i.e. interruption of signal reception). Three classes of signal quality were described. ‘Regular beep - resting at the surface’ corresponds to signals without any transmission breaks over a longer period (>20 seconds). ‘Intermittent beep – diving’ describes periods during which the penguin undertakes frequent dives or dive bouts (no signal) with considerable resting phases (signal for 10-20 seconds). ‘Infrequent beep – travelling’ applies to signal transmissions that are irregular and at times hard to locate; the penguin mainly dives horizontally, close to the surface (travelling) and emerges only for brief periods, resulting in just a few beeps before the transmitters aerial is submerged again.
Time accuracy
The bearings on individual penguins had to be taken more or less synchronously to reduce errors. Bearings on individual penguins were accepted as ‘synchronous’ if they were taken within 10 minutes. For that reason every station had to record the precise time of bearing (in minutes).

Pre-amplified
To get an idea of the signal’s strength and therefore an indication of the penguin’s distance to the receiving station, the need to use of the pre-amplifier was noted.

Compass rose calibration
The operator had to take an hourly bearing on the reference transmitter (see above). With the azimuth recorded it was later possible to establish a correction factor for the bearings on penguins.

Data analysis
To calculate the coordinates, analyze and plot penguin positions I used “Matlab for Windows” (Matlab 5, The Mathworks Inc.). The tracking data were transferred from the data sheets used in the field into spreadsheets using Microsoft Excel 97. Correction factors for recorded azimuths (differences between real and recorded bearing on reference transmitters) were applied in Excel. The spreadsheets were then exported as plain ASCII-matrices which in turn could be imported in Matlab for further procession.

First analysis
Before calculation of position coordinates, all recorded azimuths were checked to determine if they were taken within an appropriate time frame. I set the maximal acceptable difference for ‘synchronous’ bearings as 10 minutes. The preferred swimming speed of Little Penguins was determined in previous studies to be 1.8 m/s (Bethge et al. 1997). Swimming at this speed a penguin performing a continuous horizontal dive would be travel a distance of 1080 m in 10 minutes. This value lies within the range of the average location error (see above) and was considered acceptable. The 10-minute timeframe is a compromise between accuracy of position fixes and practicability of this method of data collection. Diving behaviour of some penguins or weather conditions can complicate tracking so that even when attempting to take synchronous bearings, the readings were often 5 minutes or more apart.
Calculating coordinates of position fixes

The position fixes were calculated through basic triangulation of the recorded azimuths at both stations with the known length of the baseline. However, basic triangulation relies on the isometric distribution of all known coordinates. For that reason the geographic coordinates of the receiving stations that were recorded as longitude/latitude pairs had to be converted into isometric "New Zealand Grid Map" values. This was done with the software "Geographic Calculator 4.2" (Blue Marble Geographics, http://www.bluemarblegeo.com).

Second analysis

After calculating position fixes, the coordinates of the consecutive fixes formed a route or track a penguin used during the day. A second analysis was necessary to validate the coordinates of the position fixes. Firstly, horizontal swimming speeds between consecutive position fixes were calculated (using linear distance and time difference between consecutive fixes). If a penguin had to swim faster than 3.3 m/s (maximal swimming speed for Little Penguins – Bethge et al. 1997) to get from position A to position B, the latter position was rejected. In that case the speed calculation was repeated using position A and position C (the position following the rejected one). Some inappropriate positions could be determined visually (if a position lay far outside the travel route indicated by the other points). Secondly, parameters 'Null width' and 'signal quality' of position fixes were checked. If these parameters indicated bad reception properties (broad null width, infrequent beeps) the position fixes were rejected if in doubt.

In addition to the analysis that was necessary to reconstruct penguin tracks, the data were used to determine horizontal travelling speeds (speeds between accepted position fixes), total distance travelled during the day, and distances between every position fix and a penguins' home colony (foraging radius).

Plotting penguin tracks

Penguin tracks were plotted in Matlab 5. As a first step, coastline data of both study areas – which is available on WWW as coordinate sets of vector points ("Coastline Extractor", Rich Signell, U.S. Geological Survey, http://riminator.ngdc.noaa.gov/coast/) – was converted to the isometric New Zealand Grid Map (NZGM) using the "Geographic Calculator". Than the Matlab toolbox "Mapstuff" (Rich Signell 1997, U.S. Geographical Services,
http://crusty.er.usgs.gov/sea-mat/mapstuff-html/) was used to plot the converted coastline data. Finally, accepted position fixes and specific linear connections between the fixes were added to this plot.

To visualize missing or rejected, fixes two different line formats that connected consecutive positions were used. Solid lines mark sections of penguin tracks with consecutive position fixes that were recorded within the pre-set interval of bearings. Dashed lines indicate missing or rejected fixes between connected positions. Dash-dot lines link the last position fix of a previous day with the first position fix of the next day (if the penguin performed a trip of two days or more).

In general, position fixes that mark full or half hours are plotted as grey boxes and labelled with the corresponding time of day. A yellow box indicates the first position fix of a day; a red box indicates the last position fix of a day. A yellow circle marks the last position of the previous day (on trips lasting two or more days). All other position fixes are plotted as “x”.

All plots were exported as image files (Tagged Image File Format – TIFF). To add depth contours, each plot was edited using image editing software (Paint Shop Pro 7, Jasc Software Inc.). Scanned bitmap images of nautical charts of both study areas were transformed to vector images, resized accordingly and superimposed on each plot. The merged images were then exported as Tagged Image Format.
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1.7 REFERENCES


<table>
<thead>
<tr>
<th>TIME</th>
<th>AZIMUTH</th>
<th>NULL WIDTH</th>
<th>SIGNAL QUALITY</th>
<th>TIME ACCURACY</th>
<th>PRE-AMPLIFIED</th>
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<td>Scheduled time</td>
<td>3 digits always (eg. 2° = 002)</td>
<td>0 = No Signal</td>
<td>0 = No Signal</td>
<td>Insert exact time (minutes) of bearing</td>
<td>0 = no pre-amp</td>
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<tr>
<td>(New Zealand Standard Time)</td>
<td>1 = Null &lt; 003°</td>
<td>1 = Regular beep (resting at surface)</td>
<td><strong>1 = with pre-amp</strong></td>
<td></td>
<td></td>
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<tr>
<td>2 = Null 003° to 012°</td>
<td>2 = Intermittent beep (diving)</td>
<td>2 = Null 012° or No Null</td>
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<td></td>
<td></td>
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<tr>
<td>3 = Broad Null &lt; 012°</td>
<td>3 = Infrequent beep (traveling)</td>
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**Animal I.D.**

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Appendix III

Detailed chick-growth curves

Chick growth determined at Oamaru; weights taken from 57 A-chicks and 38 B-chicks

Chick growth determined on Motuara Island; weights taken from 17 A-chicks and 7 B-chicks