THE BREEDING ECOLOGY OF THE NORTH ISLAND LITTLE SHEARWATER,
Puffinus assimilis haurakiensis.

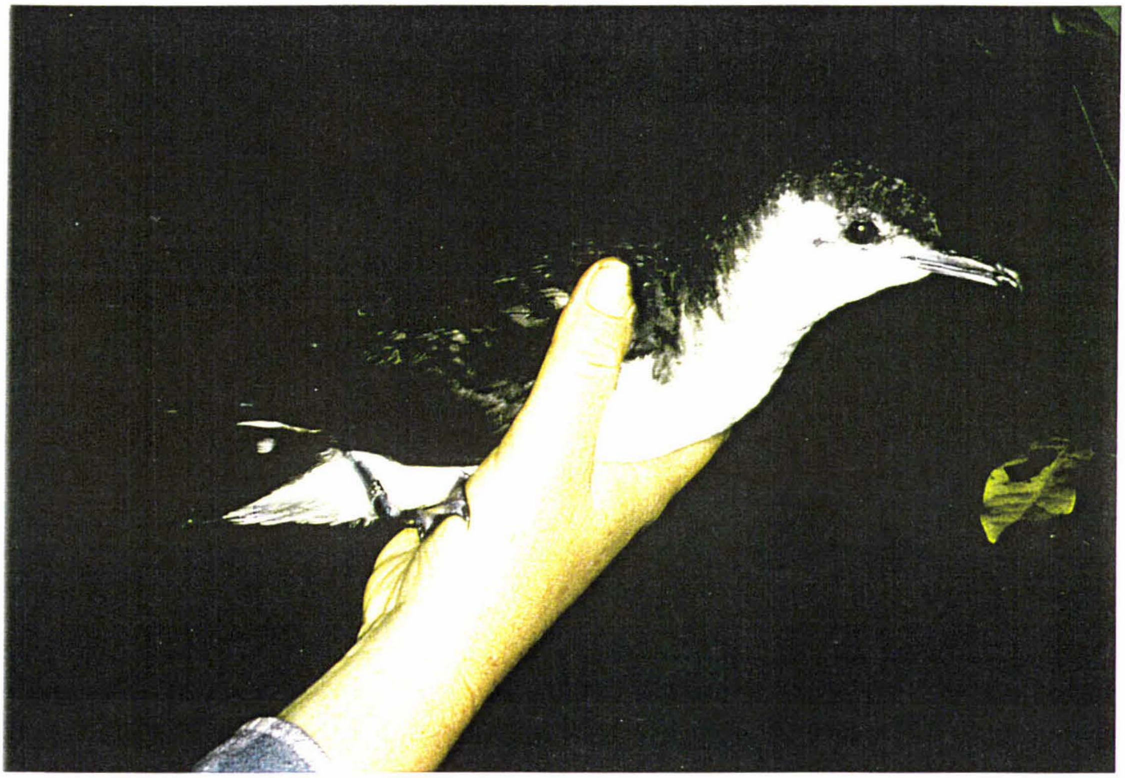
A thesis presented in partial fulfilment
of the requirements for the degree of

Master of Science in Ecology

at Massey University.

Andrea Marie Booth

1996



Frontispiece: North Island Little Shearwater (*Puffinus assimilis haurakiensis*), Lady Alice Island, Hen and Chickens Group, New Zealand, 1994.

ABSTRACT

The breeding ecology of the North Island Little Shearwater *Puffinus assimilis haurakiensis* was investigated on Lady Alice Island, Hen and Chickens Group, Northland, New Zealand, during the 1994 breeding season.

The Little Shearwater showed a high degree of intra-population asynchrony in laying compared to other procellariiform species. This suggests that there is not an optimum time for laying in this species, and that laying is influenced by a low variability in the food supply during the breeding season.

The behaviour of Little Shearwater breeding adults was monitored throughout the chick rearing period. Chicks were fed, on average, on 96% of nights. This result is not compatible with the theory that large fat deposits in procellariiform chicks are an adaptation to a fluctuating food supply.

Parents coordinated their feeding sessions, with one bird at a time feeding the chick for approximately seven night in a row. This strategy may result in less variation in the food provisioning rate compared with records for other Procellariiformes, in which adults forage independently. If this is so, coordination of foraging sessions does not support the hypothesis that fat deposits in Little Shearwater chicks provide insurance against variation in the food delivery rates of parents. Coordination of foraging shifts may allow adults to obtain more accurate information about the nutritional status of the chick, and therefore regulate meal size according to chick requirements. Little Shearwater chicks lost a smaller proportion of their body mass between obtaining maximum chick mass and fledging (17.7%), than other species in the family Procellariidae. This observation is compatible with adults regulating the amount of food delivered to chicks. Adults do not appear to feed chicks at the maximum rate possible for parents, as has been suggested for species which forage independently. Further research is required to determine the factors influencing both fat deposition in chicks, and adult foraging behaviour in the Little Shearwater.

Little Shearwater burrows were monitored throughout the breeding season for signs of predation by kiore, *Rattus exulans*. Direct evidence of kiore predation of eggs was obtained by timelapse video. The breeding success rate of Little Shearwaters was 38% (n = 29), The majority of breeding failure occured during incubation, with 16 (89%) of the 18 unsuccessful nests failing at this stage. Kiore predation of eggs was the suspected cause of failure for at least 12 (75%) of the nests which failed at incubation. The long-term impact of kiore predation on the Little Shearwater, and the implications of these findings for management, are discussed.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the ongoing help and support of my two supervisors, Ed Minot and Robin Fordham. Like myself, procellariiform ecology was a new field for both of them, and throughout the whole thesis process they shared my enthusiasm for learning more about this fascinating and relatively unknown group of birds. I would especially like to thank Ed for being there when I had 101 questions during the writing stage, and Robin for his ideas, and braving treacherous weather to visit my study site.

I would like to thank Mike Imber for initially suggesting the topic and getting the project underway, helping with fieldwork, and sharing his extensive knowledge of Procellariiformes. John Warham, Kerry-Jane Wilson, and Brian Bell all gave their time to comment on my project proposal and make suggestions for improvement. This thesis also benefitted from discussions with the late George Dunnet.

I would like to thank the Department of Conservation, Northland Conservancy, for giving me permission to work on Lady Alice Island. Many thanks to Ray Pierce, who helped in many ways throughout the fieldwork period, and was always available to discuss aspects of the study. I also thank Keith Hawkins and the rest of the Whangarei Field Centre staff, for providing boat transport, accomodation, and general assistance.

Many thanks to my intrepid field assistants: Ina May, Peter Graham, Dagmar Ohlfest and Peter Elliott, who freely gave their time and energy to help me in the field, and didn't complain when I made them carry 22kg batteries up hills.

Students and staff of the Ecology Department, Massey University, helped throughout this study. I would especially like to thank Rosemary Miller for her support and commenting on drafts of the thesis, Barbara Just for assistance with equipment and accounts, Liz Grant for the drawing of the kiore, Jens Jorgesen for his engineering skills, and Isabel Castro and Phil Battley for bird discussions, although they still haven't realised that seabirds are much more interesting than bush birds and waders.

Thanks to Paul Jansen for making and lending the video equipment, and John Innes for his comments on kiore predation.

A very special thanks to my family, for their ongoing encouragement and support over the last two years - mum, Jacqui, Brendon, Jesse, Caitlin, Kathleen, Nicky, and Jim. Also to Eric Allen, who made the final writing stage much more bearable by his patience and encouragement.

Funding for this project was gratefully received from the Massey University Graduate Fund, the Massey Ecology Department, the Royal Forest and Bird Protection Society of New Zealand, and the Ornithological Society of New Zealand.

TABLE OF CONTENTS

Chapter One: Introduction

Chapter Two: The Pre-laying Behaviour and Incubation Period of the Little Shearwater

Chapter Three: The Chick Rearing Stage of the Little Shearwater

Chapter Four: Little Shearwater Breeding Success, and Evidence of Predation by Kiore, *Rattus exulans*

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

Chapter One: Introduction

1.1 General Introduction

Shearwaters are members of the order Procellariiformes, which includes the albatrosses, petrels, fulmars and prions. Most Procellariiformes are pelagic feeders, and have a low reproductive rate and a high life expectancy. The breeding ecology of this family is characterised by a high degree of faithfulness to the nest site and mate, with incubation and chick rearing usually shared equally by the two parents. Females lay a single egg, and there are no second clutches. The breeding season is long, compared to birds of a similar size (Warham 1990).

Following several long-term studies of other *Puffinus* species (eg. *P. puffinus* (Brooke 1990), *P. tenuirostris* (Bradley *et. al.* 1991)), the breeding ecology of this genus has been well documented, and generally parallels the breeding patterns typical of Procellariiformes. Details of the breeding ecology of the Little Shearwater, however, are sparse. Like most *Puffinus* species, the Little Shearwater is not active at the breeding site during the day, but returns only at night to relieve its partner of incubation or to feed the chick. In New Zealand waters, Little Shearwaters breed only on offshore islands, and the nest is built in a chamber at the end of an often inaccessible burrow. Together, these factors have made studying the Little Shearwater somewhat difficult.

Information about the breeding ecology of the Little Shearwater is important in that it increases our understanding of general procellariiform ecology and breeding systems, and is also an aid in future management decisions concerning this species. Knowledge of the timing of incubation and chick rearing, as well as strategies adopted by parents during breeding, is vital when planning management options concerning, for example, the vulnerability of the Little Shearwater to introduced predators or the potential for competition with other burrow-nesting seabirds.

1.2 Thesis Objectives

The central objectives of this thesis were to obtain information about the breeding ecology of the North Island Little Shearwater (*Puffinus assimilis haurakiensis*), and to determine the extent of impact by kiore (*Rattus exulans*) on the Little Shearwater population. The specific aims were:

1. to investigate the pre-laying behaviour and incubation period of the Little Shearwater, including the attendance and behaviour of adults at the breeding site before

laying; the pre-laying exodus; the timing of egg laying; the length of incubation shifts; weight loss by adults during incubation; and the degree of egg desertion.

2. to investigate chick rearing in the Little Shearwater, including chick hatching and brooding; chick growth; and the strategies adopted by adults during food provisioning.

3. to determine the degree of predation by kiore on eggs and chicks; the timing of predation events; aspects of Little Shearwater behaviour which influence their susceptability to predation; and the sign left by kiore after preying on eggs.

1.3 **Thesis Organisation**

Chapter One provides the thesis objectives, and background information about the Little Shearwater, including the distribution and status of Little Shearwater sub-species, a description of the species, and previous research conducted on breeding ecology. A description of the study site is also given in this chapter.

Chapters Two and Three describe aspects of the breeding ecology of the Little Shearwater. In Chapter Two I provide details of the pre-laying behaviour and incubation period. I also provide circumstantial evidence of extra-pair copulations, and discuss the possible impact of food availability on the timing of laying. Chapter Three oulines chick growth and adult behaviour during the chick rearing stage. Based on the foraging strategies of adults, I question the role of large fat deposits in chicks as insurance against stochasticity in either food availability or adult food provisioning ability. I also present a food provisioning strategy previously undescribed in Procellariiformes, whereby adults coordinate feeding shifts.

In Chapter Four, I present the first direct evidence of kiore preying on seabird eggs in New Zealand. I describe the timing of predation events, and aspects of Little Shearwater behaviour which may increase their vulnerability to kiore predation. I also describe the sign left by kiore after preying on eggs, and the possible long-term impact of kiore predation on the Little Shearwater. This chapter has been submitted to *Notornis* as a jointly authored manuscript.

Chapter Five provides a summary and conclusions of the preceeding three chapters, and outlines suggestions for further research regarding questions raised about Little Shearwater breeding ecology, and predation by kiore.

Chapters Two, Three and Four have been written as stand-alone chapters designed for publication, so there is some replication between these chapters.

1.4 **Distribution and Status**

Little Shearwaters are found in the South Indian, Pacific and Atlantic Oceans, generally north of the Antarctic Convergence, and reach the Northern hemisphere (c. 40°N) in the Atlantic Ocean. There are seven subspecies (Turbott 1990), five of which occupy the Australasian region. Northern hemisphere subspecies breed in the North Atlantic Ocean (*P. a. baroli*); and in the Austral group in the south central Pacific Ocean (*P. a. myrtae*). Southern hemisphere sub-species breed on islands off the north-east coast of the North Island of New Zealand (*P. a. haurakiensis*); on the Chatham and Antipodes Islands, the Tristan da Cunha Group, and Gough Island (*P. a. elegans*); on the Kermadec Islands (*P. a. kermadecensis*); on Norfolk and Lord Howe Islands (*P. a. assimilis*); and on offshore islands in southwest Australia. (*P. a. tunneyi*) (Fleming & Serventy 1943, Turbott 1990).

The North Island Little Shearwater, *P. a. haurakiensis*, breeds on Moturoa Island, Stephenson Island, the Cavalli Islands, the Poor Knights Islands, the Hen and Chickens Group, the Mokohinau Group, the Mercury Islands, and the Alderman Islands (Turbott 1990). *P. a. haurakiensis* ranges from about North Cape to the Bay of Plenty, and occasionally straggles as far south as Hawkes Bay (Imber 1985).

The conservation status of Little Shearwater sub-species breeding in New Zealand waters is assumed to be stable, except for *P. a. kermadecensis*, which is listed as rare (Bell 1986).

1.5 **Description**

The Procellariiformes are characterised by nostrils which are sheathed in prominent horny tubes arising near the base of the bill (Warham 1990). Members of the genus *Puffinus* have nostrils which open obliquely upwards, and laterally flattened tarsi (Robertson 1985, p309).

The Little Shearwater measures approximately 30cm long, and is the smallest of all shearwaters. The upperparts are entirely sooty black, and the underparts entirely white. The axillaries sometimes have grey spots or smudges on them. The line of demarcation between black and white on the head is above the eye, giving the Little Shearwater a white face. The bill is slender and lead-coloured, and black along the ridge and tip. The feet are blue with fleshy webs, and the claws are black (Falla *et. al.* 1978, Imber 1985). At sea, the Little Shearwater can be distinguished from the Fluttering shearwater by its more rapid wingbeats and shorter glides (Harper & Kinsky 1974). The North Island sub-species, *P. a. haurakiensis,* can be distinguished from other Little Shearwater sub-species found in New Zealand waters by a longer and stouter bill, lighter plumage, and a less well defined head pattern. The wing, tail, and mid-toe plus claw are longer than *tunneyi* and *assimilis*, and approximately equal to *kermadecensis*. The tarsus is longer than that of *kermadecensis* (Fleming & Serventy 1943).

1.6 **Breeding Ecology**

Details of the incubation and nestling periods of the Little Shearwater exist only for the Western Australian sub-species, *P. a. tunneyi* . Incubation lasts from 52-58 days (n = 4), with adults relieving each other of incubation duty about every two days (Glauert 1946). After hatching, the chick is brooded for several days, then it is abandoned by the adults during the day (Warham 1958). *P. a. tunneyi* has a nestling period of 70-75 days, with the chick being fed by both parents every second night for the first fortnight, then once or twice every five nights thereafter. The chicks then fast for 8-10 days before fledging (Glauert 1946). The Little Shearwater breeds in the winter, and is non-migratory.

In New Zealand waters, Little Shearwaters return to the colonies to mate from Febuary to May (Warham and Bell 1979; Hermes *et. al.* 1986). Eggs are laid from July (Fleming and Serventy 1943, Hermes *et. al.* 1986), but fresh eggs have been found as late as September on the Mercury Islands (Edgar 1962), and October on the Antipodes Islands (Imber 1983). Chicks usually fledge from November (Merton 1970, Tennyson *et. al.* 1989), with chicks fledging as late as mid-Febuary on the Antipodes Islands (Imber 1983). An extended season has been described for the Chathams Islands, with chicks fledging from May through October (Bourne 1980).

1.7 **Study Site**

Lady Alice Island (138 ha, 35°54'S, 174°44'E), is the largest of the Chickens Islands in the Hen and Chickens Group (Figure 1.1). Access to all of the islands in this group is restricted. Although Lady Alice Island has been modified in the past by Maori occupation, cattle grazing and fires (Percy 1955), it currently supports a diverse flora (Percy 1955, Jane & Beever 1965, Cameron 1984). The valleys follow a transition from flax (*Phormium tenax*) and coastal scrub in the lower reaches through kohekohe (*Dysoxylum spectabile*) -puriri (*Vitex lucens*) forest to pohutukawa (*Metrosideros excelsa*) - puriri forest at the heads of the valleys. Ridges are dominated by kanuka (*Kunzea ericoides*) (Percy 1955). Research was conducted at four study sites on Lady Alice Island. The vegetation type at each of the four study sites is shown in Plates 1.1 to 1.4. Bird surveys on Lady Alice Island have been conducted by (Skegg 1964) and

McCallum *et. al.* (1984). Four species of procellariid seabirds breed on Lady Alice Island - Little Shearwaters and Grey-faced Petrels (*Pterodroma macroptera*) in the winter; and Pycroft's Petrels (*Pterodroma pycrofti*) and Flesh-footed Shearwaters (*Puffinus carneipes*) in the summer. Tuatara (*Sphenodon punctatus*) are present in densities near the lower limit of the range observed on rat-free islands (Crook 1973). Kiore were present on Lady Alice Island until 27 October, 1994, when they were eradicated by an aerial poison drop. It is not known how long kiore had been on this island (R. J. Pierce, *pers. comm.*)

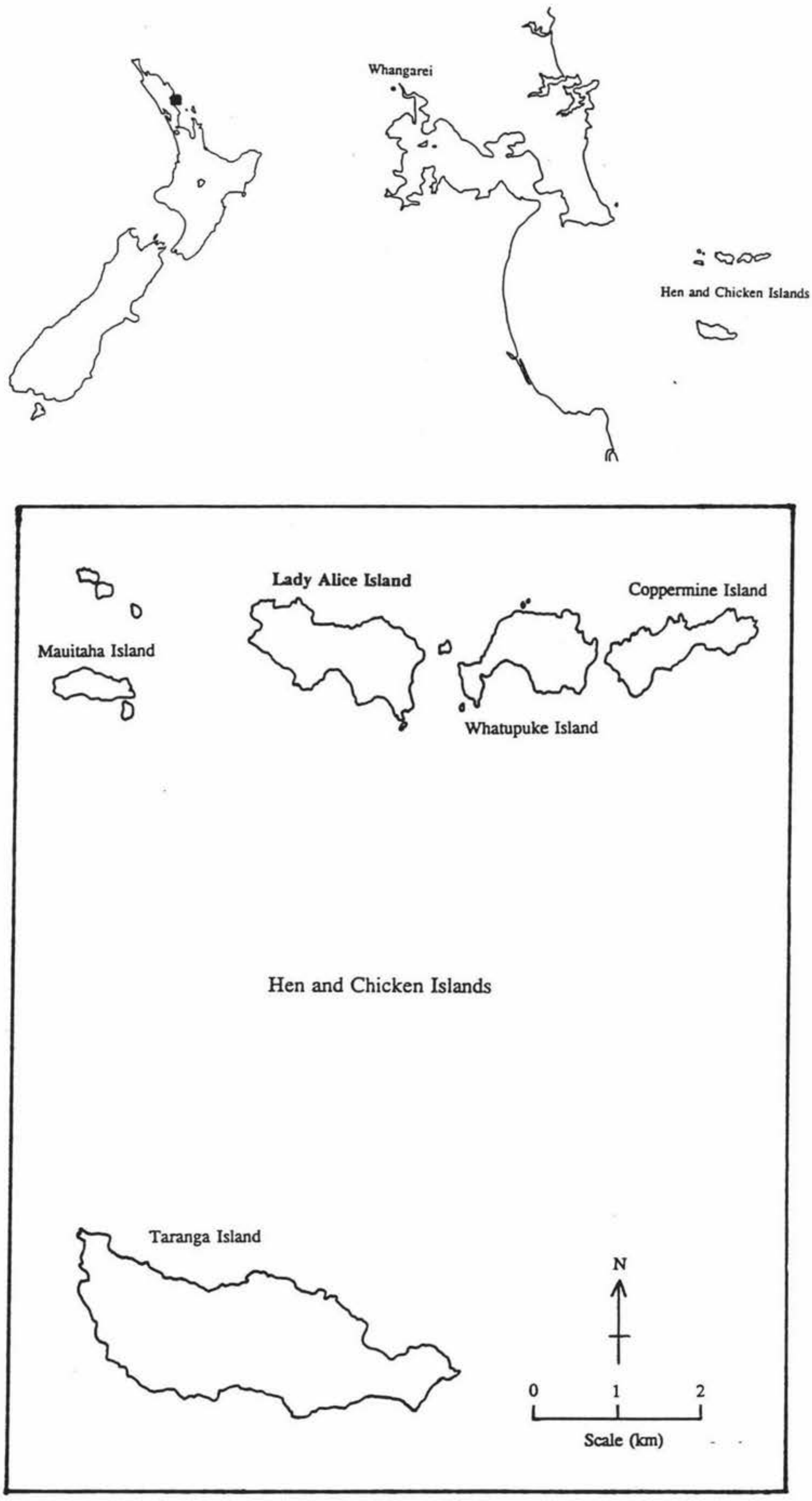


Figure 1.1: Location of Lady Alice Island, Hen and Chickens Group, in relation to Whangarei, Northland, New Zealand.

Plate 1.1: Vegetation type at the Hut Site (site 1), Lady Alice Island.

Plate 1.2: Vegetation type at the Gully Site (site 2), Lady Alice Island.

Plate 1.3: Vegetation type at the Ridge Site (site 3), Lady Alice Island.

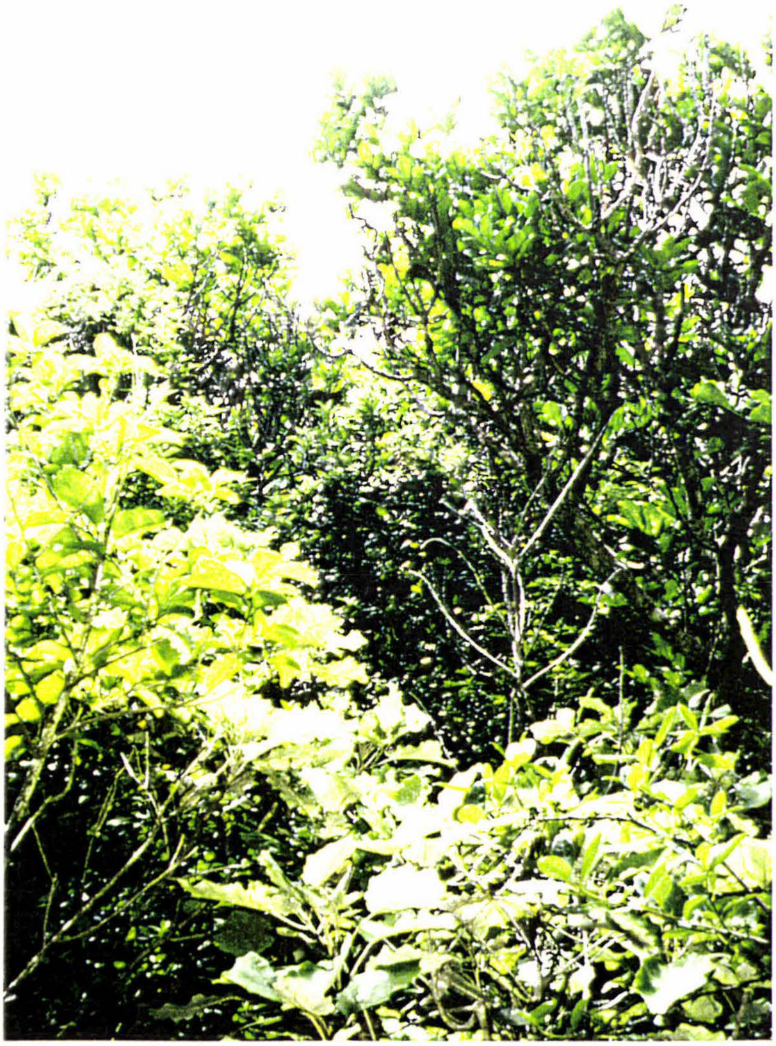


Plate 1.4: Vegetation type at the Pa Site (site 4), Lady Alice Island.

1.8 References

Bell, B.D. 1986. The conservation status of New Zealand wildlife. New Zealand Wildlife Service Occasional Publication No. 12; Department of Internal Affairs, Wellington.

Bourne, W.R.P. 1980. The prions collected by R.H. Beck off the Antipodes Islands and the breeding season of the Little Shearwater. Notornis 27: 297-298.

Bradley, J.S.; Skira, I.J.; Wooller, R.D. 1991. A long-term study of Short-tailed Shearwaters *Puffinus tenuirostris* on Fisher Island, Australia. Ibis 133 suppl.1: 55-61.

Brooke, M. 1990. The Manx Shearwater. Poyser: London.

Cameron, E.K. 1984. Vascular plants of the three largest Chickens (Marotere) Islands: Lady Alice, Whatupuke, Coppermine: North-east New Zealand. Tane 30: 53-75.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20: 115-120.

Edgar, A.T. 1962. A visit to the Mercury Islands. Notornis 10: 1-15.

Falla, R.A.; Sibson, R.B.; Turbott, E.G. 1978. Collins Guide to the Birds of New Zealand. HarperCollins Publishers (New Zealand) Limited: Auckland.

Fleming, C.A.; Serventy, D.L. 1943. The races of *Puffinus assimilis* in Australia and New Zealand. Emu 43: 113-125.

Glauert, L. 1946. The Little Shearwater's Year. Emu 46: 187-192.

Harper, P.C.; Kinsky, F.C. 1974. New Zealand albatrosses and petrels. An identification guide. Tuatara 21: 42.

Imber, M.J. 1983. The lesser petrels of Antipodes Islands, with notes from Prince Edward and Gough Islands. Notornis 30: 283-298.

Imber, M.J. 1985. Little Shearwater. Pages 101 *in* Robertson, C.J.R. (ed.) The Reader's Digest Complete book of New Zealand Birds. Sydney: Reader's Digest Services Pty Ltd.

Jane, G.; Beever, R.E. 1965. A list of the vascular plants of Motu Muka (Hen and Chickens Group). Tane 11: 87-91.

McCallum, J.; Bellingham, P.J.; Hay, J.R.; Hitchmough, R.A. 1984. The birds of the Chickens Islands, northern New Zealand. Tane 30: 105-124.

Merton, D.V. 1970. Kermadec Island expedition reports: a general account of birdlife. Notornis 17: 147-199.

Percy, C.A. 1955. A primary study of the vegetation of Marotiri Island. Tane 7: 3-6.

Robertson, C.J.R. 1985. The Reader's Digest Complete Book of New Zealand Birds. Reader's Digest Services Pty Ltd: Sydney.

Skegg, P.D.G. 1964. Birds of the Hen and Chickens Islands. Notornis 11: 159-182.

Tennyson, A.; Taylor, G.; Scofield, P. 1989. Another visit to Macauley Island. OSNZ News 52: 4-5.

Turbott, E.G. 1990. Checklist of the Birds of New Zealand. Random Century In association with the Ornithological Society of New Zealand:

Warham, J. 1958. Photographic studies of some less familiar birds. XCII Little shearwater. British Birds 51: 393-397.

Warham, J. 1990. The petrels, their ecology and breeding systems. Academic Press: London.

Chapter Two: The pre-laying behaviour and incubation period of the Little Shearwater

2.1. Introduction

There are seven subspecies of Little Shearwater (Turbott 1990), none of which have been studied in detail. Unlike most of the Procellariiformes, Little Shearwaters breed in the winter, possibly to avoid competition for food resources with summer breeding seabirds (Warham 1990). They are non-migratory, and may reduce competition for food with summer breeders by foraging over a greater distance during the summer months (Warham 1990). The time at which Little Shearwaters first return to the breeding ground is unknown, and is likely to be poorly defined due to the non-migratory nature of the species (Warham 1990). After mating, procellariiforms return to sea until it is time to lay. This period has been termed the "pre-laying exodus", during which the female builds up food reserves in order to form the single egg, and the male stores food for the first incubation shift (Lack 1966). The length of the pre-laying exodus varies between *Puffinus* species. Manx Shearwaters (*P. puffinus*) are absent from the breeding site for about 14 days after mating (Perrins & Brooke 1976), while Buller's Shearwaters (*P. bulleri*) have a pre-laying exodus of about 30 days (Harper 1983). There is no published record of the length of the pre-laying exodus of the Little Shearwater. Like most other shearwaters, the egg is laid in a burrow and incubation is shared by both members of the pair, which undertake long, alternating shifts throughout incubation. Glauert (1946) recorded a mean incubation period of 54 days for the Western Australian subspecies *P. a. tunneyi*, but the length of each incubation shift and the rate at which adults lose weight during incubation has not been studied in detail.

In this chapter, I present details of the pre-laying behaviour and incubation period of the North Island Little Shearwater *P. a. haurakiensis*. I describe the activity of adults at the breeding site before incubation commences, including the length of the pre-laying exodus, and present circumstantial evidence that Little Shearwaters engage in extra-pair copulations. I present information on the period over which eggs are laid and the size of eggs, and discuss these data in relation to food availability during the winter breeding season. I also describe the length of incubation shifts by each parent, the rate of weight loss by each parent during incubation shifts, egg weight changes, and the total length of the incubation period. Finally, I discuss the degree of temporary egg desertion in the Little Shearwater.

2.2. Methods

2.2.1 Study Site

Lady Alice Island (138 ha, 35°54'S, 174°44'E), is the largest of the Chickens Islands in the Hen and Chickens Group. Access to all of the islands in this group is restricted. Although Lady Alice Island has been modified in the past by Maori occupation, cattle grazing and fires (Percy 1955), it currently supports a diverse flora (Percy 1955, Jane & Beever 1965, Cameron 1984). The valleys follow a transition from flax (*Phormium tenax*) and coastal scrub in the lower reaches through kohekohe (*Dysoxylum spectabile*) - puriri (*Vitex lucens*) forest to pohutukawa (*Metrosideros excelsa*) - puriri forest at the heads of the valleys. Ridges are dominated by kanuka (*Kunzea ericoides*) (Percy 1955). Bird surveys on Lady Alice Island have been conducted by (Skegg 1964) and McCallum *et. al.* (1984). Four species of procellariid seabirds breed on Lady Alice Island - Little Shearwaters and Grey-faced Petrels (*Pterodroma macroptera*) in the winter; and Pycroft's Petrels (*P. pycrofti*) and Flesh-footed Shearwaters (*Puffinus carneipes*) in the summer. Tuatara (*Sphenodon punctatus*) are present in densities near the lower limit of the range observed on rat-free islands (Crook 1973). Kiore were present on Lady Alice Island until 27 October, 1994, when they were eradicated by an aerial poison drop. It is not known how long kiore had been on this island (R. J. Pierce, *pers. comm.*).

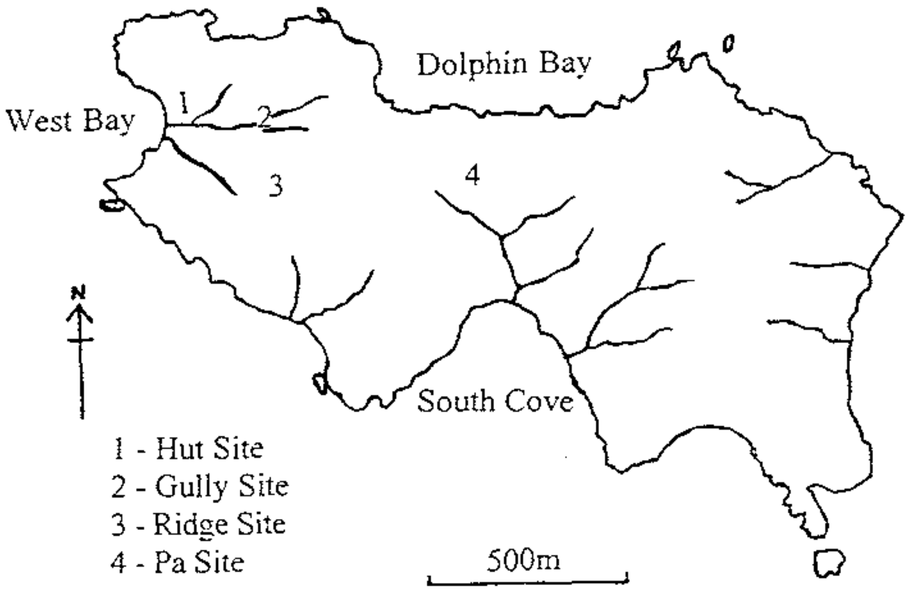


Figure 2.1: Location of study sites on Lady Alice Island.

2.2.2 Pre-laying behaviour

During 1994, five trips were made to the study site during the pre-laying and incubation periods: 14 - 22 June, 19 - 29 July, 16 - 30 August, 12 - 26 September, and 12 - 21 October.

Burrows monitored during the study lay within one of four study sites on Lady Alice Island (Figure 2.1). All burrows were first checked on 14 June for signs of use by Little Shearwaters. A 'fence' of fine sticks was placed over each burrow entrance, and subsequently checked and replaced daily. The fences were fine enough not to restrict birds entering burrows. When a fence was disturbed, the nesting chamber was checked for occupation by carefully inserting a stick, or by looking through the observation hole. Burrows were also checked daily for signs of nest building, such as an accumulation of nesting material around the burrow entrance.

For active burrows where I could not gain access to the nesting chamber, an observation hole was dug into the burrow just in front of the nesting chamber. Observation holes were never dug directly above the nest chamber, so that debris and strong light did not enter the chamber when the hole was in use. Observation holes were covered by round rocks, and the edges of the holes filled with soil and leaf litter to reduce the entry of rain and light. Each burrow was checked daily for occupancy. All birds found in the burrows were banded, and weighed to the nearest gram using a Pesola spring balance. The following measurements were taken with vernier calipers accurate to 0.1mm: culmen length, tarsus length, mid-toe + claw length, and tail length. The unflattened wing length was measured to the nearest mm using a flanged ruler. Areas with active burrows were also searched at night, and any new birds captured on the ground were banded, weighed and measured.

2.2.3 Incubation

Birds were sexed by cloacal examination (Serventy 1956) or by attendance at the nest at the start of the incubation period. Females were identifiable by a swollen, reddened cloaca. Birds with a ‘normal’ cloaca, which incubated for the first shift after egg laying, were assumed to be males. When the sex of a bird was uncertain, I waited until the second member of the pair was captured so that cloacal sizes could be compared. If sex could still not be determined from cloacal size, birds were left unsexed.

If eggs were laid while I was present at the study site, laying dates and adult weights at laying were recorded. When the egg laying dates were unknown, they were estimated at the end of the incubation period by one of two methods. If the date of hatching was known, the laying date was estimated by subtracting the average incubation period from the hatching date. Alternatively, the days elapsed since laying were estimated by determining which incubation shift was being undertaken when an incubating bird was first found, then subtracting the average length of all previous incubation shifts before that date by using data from other nests. The length and width of eggs were measured using vernier calipers accurate to 0.1mm.

When burrows contained incubating Little Shearwaters, fences were maintained across the entrances throughout the incubation period and checked daily. Burrows with displaced fences were checked for occupancy by looking through the observation lid, or by inserting a stick into the nesting chamber. Incubating birds were removed from the burrow and, on average, weighed every second day. As bird approached the end of its incubation shift, it was removed, weighed, and its band checked whenever the fence was found to be displaced. This procedure ensured that the date of changeover and the weight of the new bird at the start of the incubation shift were recorded. When an egg was left unattended, the nesting chamber was checked daily until a Little Shearwater adult returned to incubate. Eggs were not weighed regularly during the incubation period because of the small sample size and the risk of breakages during handling.

2.2.4 The Effects of Investigator Disturbance

To determine the effect of investigator disturbance on Little Shearwater breeding success, a group of control burrows was established at each site. The control burrows were known to contain incubating Little Shearwater adults at the start of the breeding season. These burrows were not monitored during the study until the end of the breeding season, when they were checked for the presence of Little Shearwater chicks. Adults were not removed from the control burrows at any stage of the study. The control burrows could not be selected at random because the total number of burrows with eggs was low. Burrows with inaccessible nest chambers were chosen as control burrows. At the end of the study, the breeding success of Little Shearwater pairs in control and monitored burrows was compared.

Unless stated otherwise, results are given as the mean ± 1SD.

2.3. **Results**

2.3.1 Pre-laying behaviour

Little Shearwaters were found in burrows on Lady Alice Island from 14 June 1994 onwards. I was present at the breeding site for three days in mid-March 1994, but no birds were seen or heard at this time. Birds were probably present before June, as on Coppermine Island, also in the Hen and Chickens group, Little Shearwaters were heard calling from burrows in mid-March 1995 (*pers. ob.*). The estimated timing of first arrival at the colony and nest excavation is shown in Figure 2.2. In order to determine the time of first arrival at the breeding site by Little Shearwaters, trips to the breeding site should be made from early March onwards.

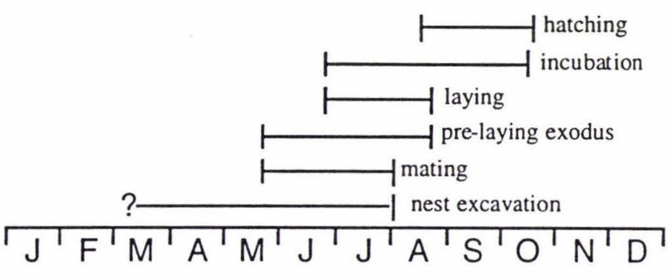


Figure 2.2: Timing of Little Shearwater breeding activity during the pre-laying and incubation periods.

Burrows used by Little Shearwater pairs showed signs of nest building from mid to late June onwards. Characteristic sign included a build-up of twigs and leaf-litter around the burrow entrance (Plate 2.1). Other signs indicating a burrow was in use for breeding included soil excavated from the nesting chamber to the burrow entrance, fresh droppings outside the burrow entrance, and the building of a nest in the nesting chamber.

The mean weight of Little Shearwater adults during the pre-laying period was 221 ± 0.6g (± SE) (range = 183 - 247, n = 25). Fifteen of the weighed adults were later sexed during the incubation period. The mean weight for females (224 ± 2.9g (± SE)) did not differ significantly to that of males (220 ± 1.2g (± SE)) during the pre-laying period (Mann-Whitney U = 33, n = 7,8, n.s.).

The period during which Little Shearwaters were mating was estimated by subtracting the mean length of the pre-laying exodus (see below) from the dates that the first and last known eggs were laid. Birds were mating from approximately 21 May to 22 July in 1994 (Figure 2.2). Pairs of birds were never found together in a burrow during the mating period for more than one day or two nights. One member of each of three known breeding pairs was found alone in, or near, its breeding burrow over a month before mating. Each of these birds was male, and was present between 36 and 38 days before mating.

The number of days between the last known visit of a pair to the nest, and egg laying, was recorded for six pairs of Little Shearwaters. The average length of this pre-laying exodus was 33 ± 0.84 days (range = 29 - 35). For pairs for which the date of the last visit to the nest during mating was unknown, the start of the pre-laying

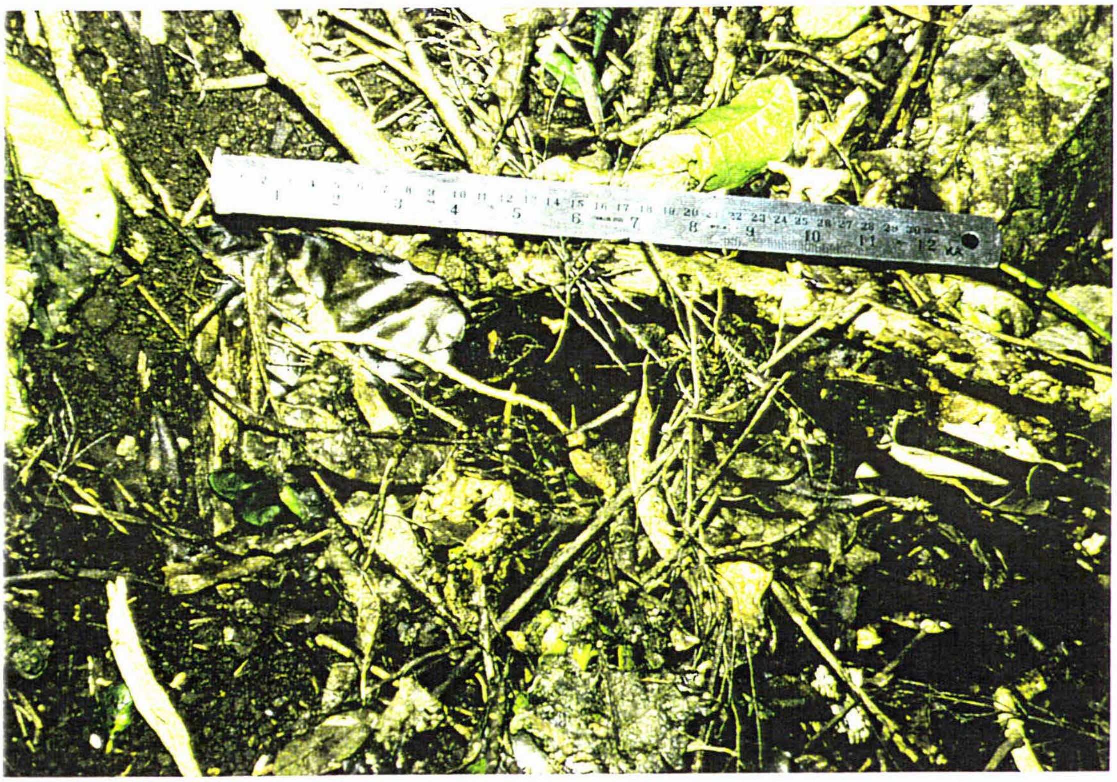


Plate 2.1: Little Shearwater burrow entrance, Lady Alice Island, June 1994. Note build-up of leaves and twigs around entrance, which is characteristic of burrows in which a nest is being built by a breeding pair.

exodus was estimated by subtracting the mean pre-laying exodus length from the date of laying. The pre-laying exodus extended from approximately 22 May to 24 August (Figure 2.2).

2.3.2 Incubation

Little Shearwaters laid in 36 of the burrows at the four study sites. Twenty six of these nests were monitored during the incubation period, and ten were used as control burrows.

For all except one of the study burrows both members of the breeding pair were captured and banded. In the remaining burrow, neither adult was captured, though an egg was subsequently laid. Twenty four (92%) of the 26 pairs of birds monitored were sexed during the start of the incubation period. The remaining two pairs were found too late in the incubation period to be sexed accurately.

Of the 26 study burrows, the exact date of laying was recorded for eight pairs of Little Shearwaters, and the estimated date of laying was calculated for 15 pairs. Laying dates were unknown for the remaining three burrows. Little Shearwaters laid their eggs over a period of 62 days, from 23 June to 24 August (Figure 2.2). The distribution of known and estimated egg-laying dates is shown in Figure 2.3. Approximately half (52%) of the eggs were laid in the first 3 weeks of the laying period. Most (83%) of the eggs had been laid by the end of July, then the remaining eggs were laid during a second laying period in the third week of August.

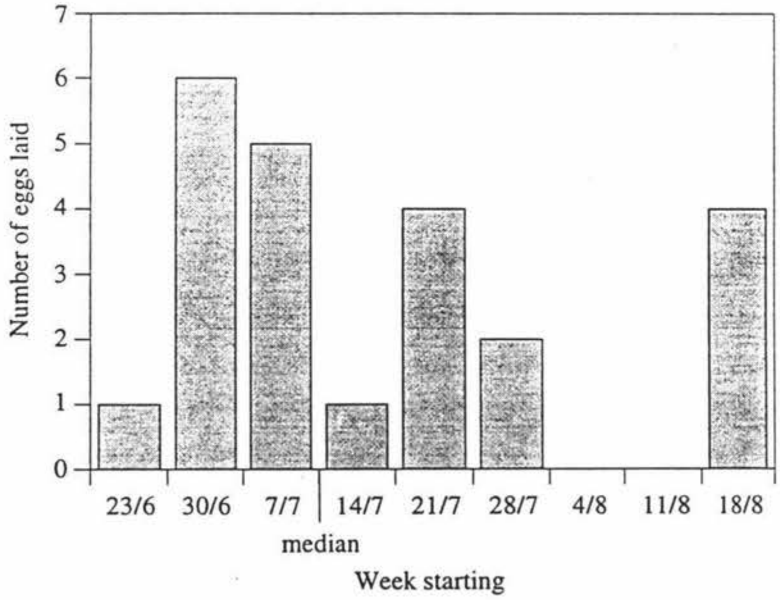


Figure 2.3: Distribution of Little Shearwater egg laying dates.

On two separate occasions during the pre-laying period, a breeding adult was found in a burrow with a bird with which it did not later share incubation of an egg, which suggests that Little Shearwaters engage in extra-pair copulations. The first pair (X4599 = male, X10417 = female) was observed copulating in a burrow during the day. X4599 was then recaptured 34 days later, incubating a freshly laid egg with a new female (X4598) in a burrow 8.5m away from the first burrow. X4599 and X4598 had also bred together in this burrow during the 1992 breeding season (M. Imber, *unpub.*). The female X10417 was recaptured 35 days later in a burrow 1.5m away from the burrow in which the extra-pair copulation was suspected. No egg was laid in this burrow during the study period.

The second pair of Little Shearwaters (X5337 = male, X10420 = female) was found at night in a burrow from which mating calls were heard. The female X10420 was found in the same burrow 31 days later with a new male (X10415). It is likely that she copulated successfully with this second male rather than X5337, because an egg was laid and incubated by her and X10415 28 days after she was first found with X10415. The first male, X5337, was recaptured 34 days later with a new female (X10442) in a burrow approximately 10m away from the first burrow. X5337 was then recaptured again in this new burrow 32 days later, incubating a freshly laid egg. This nest failed before hatching and the female with which X5337 was incubating the egg remained unidentified.

The average egg dimensions were; length: 54.7 ± 0.37mm, (range = 51.4 - 58.0, n = 24), and width: 36.7 ± 0.21 mm (range = 33.3 - 38.6, n = 24). The range of Little Shearwater egg sizes is shown in Figure 2.4.

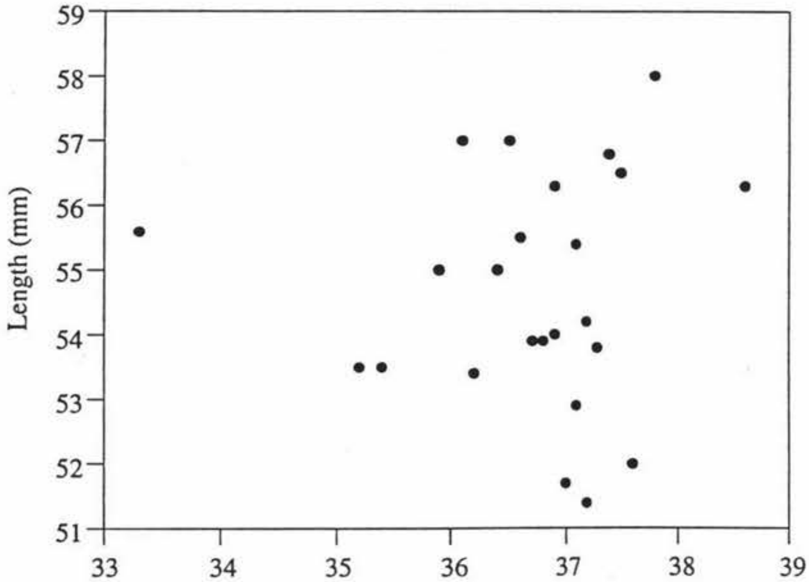


Figure 2.4: Dimensions of Little Shearwater eggs.

The mean egg weight at laying was 40 ± 3.9g (range = 35 - 46, n = 9). The rate of weight loss during the complete incubation period was recorded for only one egg.

This egg lost 0.14g/day over 52 days, or 15.2% of its original weight. During the first half of incubation, four eggs lost weight at the rate of 0.16 ± 0.08g/day (Figure 2.5).

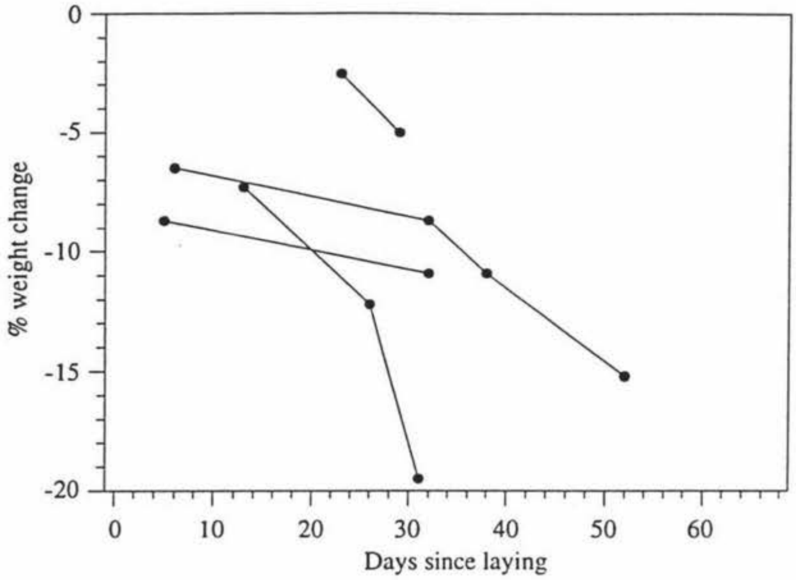


Figure 2.5: Proportion of weight change of Little Shearwater eggs during incubation. (n=4).

The egg volume index in relation to the time of laying is shown in Figure 2.6. An index of egg volume was obtained from the length multiplied by the square of the maximum breadth (Birkhead & Nettleship 1981). There was no relationship between the egg volume index and the time of laying in relation to other eggs at the study site (R = 0.03, n.s.).

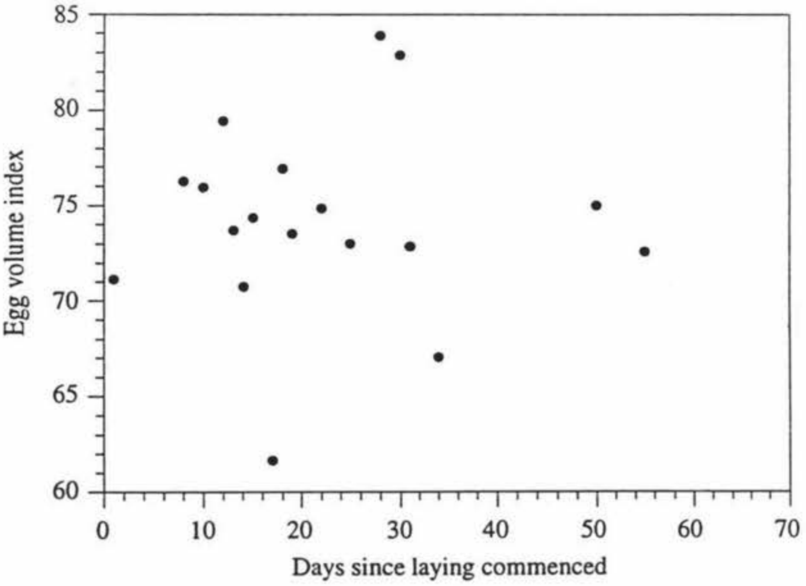


Figure 2.6: Egg volume index [length x (max. breadth)^2] of Little Shearwater eggs in relation to laying date.

Only one pair of Little Shearwaters both laid and hatched an egg while I was present on Lady Alice Island. The total length of the incubation period for this pair was 57 days. The total incubation period was estimated for pairs for which the date of either laying or hatching was known. When only the date of laying was known, the date of hatching was estimated from the size and weight of the chick using growth data from chicks of known hatching dates (Chapter 3). When only the date of hatching was known, the date of laying was estimated by subtracting the average length of previous incubation shifts from the date the incubating bird was first found, using data from other incubating pairs. The average total incubation period for Little Shearwater pairs for which laying or hatching dates were estimated was 55 ± 1.2 days (range = 54 -57, n - 3). The average length of each incubation shift and the mean rate of weight loss during each shift are shown in Table 2.1. The incubation period consisted of six or seven shifts, with the male undertaking the first shift, then the two members of a pair alternating shifts until hatching. I was present at the time of hatching for three of the nests. Two chicks hatched during shift 6 when the female was in attendance, and the other hatched during shift 7 when the male was present.

Table 2.1 Length of each shift during the Little Shearwater incubation period, and weight loss of birds for which a complete incubation shift was recorded.

Shift	Length of shift (days) mean ± SD (n)	Weight loss g/day mean ± SD	% weight loss during shift mean ± SD
1 - male	10 (1)	6.0	24.7
2 - female	8*	-	-
3 - male	9.0 ± 0.58 (3)	5.7 ± 0.37	21.5 ± 0.4
4 - female	7.5 ± 0.50 (2)	5.3 ± 0.35	15.9 ± 2.6
5 - male	10 (1)	5.4	20.3
6 - female	7.3 ± 0.67 (3)	6.5 ± 1.15	19.8 ± 4.6
7 - male	3 (1)	14.3	16.7

* The first shift by the female (shift 2) was not measured. It was estimated by subtracting the mean lengths of the other six shifts from the mean total incubation period.

Because of the low number of birds for which a complete incubation shift was recorded, I was unable to test for a significant difference between shifts in either shift length, or rate of weight loss. However, apart from shift 7, the incubation shifts of males were consistently slightly longer than those of females. Furthermore, males spent a longer time incubating overall (mean = 32 days) than females (mean = 22.8 days).

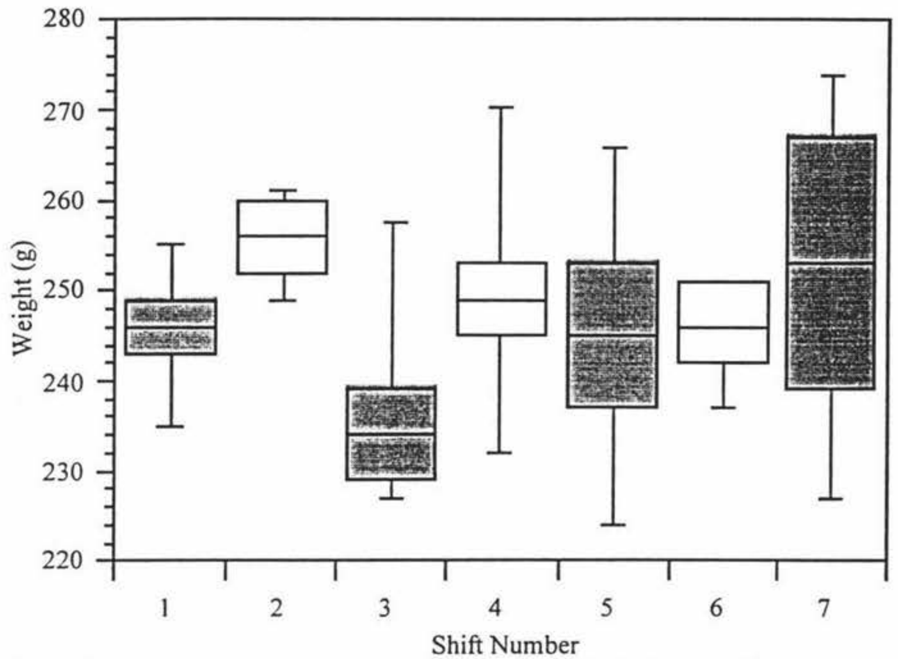


Figure 2.7: Little Shearwater male (shaded bars) and female (unshaded bars) weights at the start of each incubation shift. Horizontal lines indicate the means, rectangles are ±1SE, and vertical lines the minimum and maximum weights recorded.

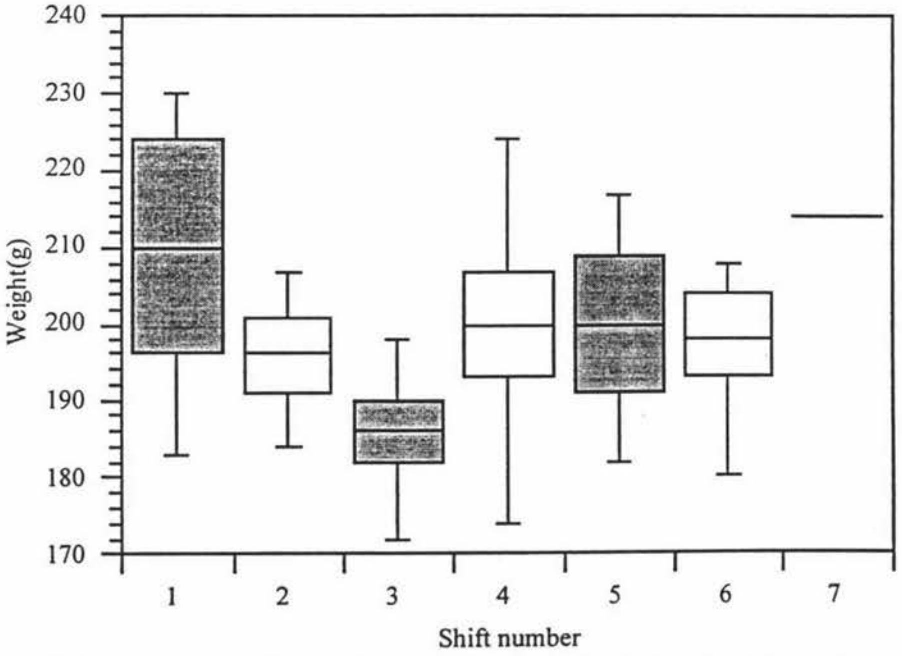


Figure 2.8: Little Shearwater male (shaded bars) and female (unshaded bars) weights at the end of each incubation shift. Horizontal lines indicate the means, rectangles are ±1SE, and vertical lines the minimum and maximum weights recorded.

The weights of birds at the start of each incubation shift are shown in Figure 2.7. Male mean weights dropped between shift 1 and shift 3, then rose again as the incubation period progressed. The mean male weight was greatest at the start of shift 7. This may have been due to males returning with a large amount of undigested food in their crops in anticipation of a hatched chick being present in the burrow, as in some burrows the chick hatched during shift 6 when the female was incubating. The mean weight of females at the start of each incubation shift decreased during the incubation period. Up to shift 7, however, the mean weight of females at the start of incubation remained higher than that of males.

The mean weights of males at the end of each shift show the same trend as mean male weights at the start of each shift (Figure 2.8). Females appeared to lose a relatively large amount of weight during their first incubation shift (shift 2), falling below the mean male weight at the end of shift 1. Mean female weights then remained steady at the end of each following incubation shift.

Eggs were left unattended for one or more days in at least 77% of the burrows. Incubating adults left the nest before being relieved by their partner in 42% of the observed changeovers (n = 33). The mean length of time that eggs were left unattended between shifts was 2 ± 1.0 days (range = 1 - 4, n = 7). In 29% of the burrows, the incubating adult left the egg unattended and then returned again. The mean period birds were away from the burrow was 1 ± 0.4 days (range = 1 - 2, n = 7). All of these birds gained weight while absent from the burrow. In one burrow, the egg was left unattended for at least seven days and still hatched. This egg was left unattended approximately six weeks after being laid. In burrows where eggs were left unattended, there was an average of 1.5 ± 0.6 periods of absence per burrow (range = 1 - 3). There was no difference between adult weight when relieved of incubation by a mate, and the weight of birds when leaving eggs unattended ($t_{22} = 0.58$, n.s.). This suggests that adults which leave eggs unattended have reached a critical minimum mass, after which they must leave the nest to feed.

The proportion and length of time that Little Shearwater eggs were left unattended by incubating adults during each week since laying is shown in Table 2.2. There was no difference between weeks in the proportion of eggs left unattended (Kolmogorov-Smirnov 2-sample test, K = 0.54, n.s.). The total number of days all eggs were left unattended was not recorded, therefore I could not determine whether the length of time eggs were left unattended differed at different stages of incubation. However, it would appear that eggs were left unattended for slightly longer periods from weeks four to six.

Four burrows may have been deserted during incubation. In three cases, the adult left after incubating for between one and four days, and at the fourth, the egg was left unattended for at least 11 days. Mean adult weight at desertion (248 ± 25.2g, n = 3) was much higher than the weight of adults when relieved of incubation (197 ± 19.2g, n = 15), suggesting that adults suspected of desertion had not reached a critical minimum mass before leaving the nest. All four of these burrows were later preyed on by kiore (*Rattus exulans*) (Chapter 4), so I could not be certain that eggs had been deserted permanently. The degree of temporary absence from the nest and of desertion may have been higher than that recorded, as burrows were not monitored continuously throughout the incubation period.

Table 2.2: The number of Little Shearwater eggs left temporarily unattended during each week after laying, and the average number of days eggs were left unattended during each week. Only eggs which were found unattended by adults during daylight hours are included.

Weeks since laying	Number of incubating pairs monitored	Number of eggs left unattended	Number of days eggs left unattended mean ± SD
1	11	7 (64%)	1.3 ± 0.2
2	6	0	-
3	13	4 (31%)	1.5 ± 0.5*
4	11	6 (55%)	2.8 ± 1.1*
5	7	3 (43%)	3.2 ± 0.9*
6	6	3 (50%)	4.0 ± 1.7*
7	10	5 (50%)	2.2 ± 1.2
8	5	2 (40%)	1.0 ± 0.0

* The number of days that eggs were left unattended may be longer than recorded, as for some of the burrows monitored, I left Lady Alice Island before either of the adults returned to incubate.

The mean number of days between pipping and hatching was 5.7 ± 2.1 (range = 4 - 8, n = 3). When the date of hatching was unknown, it was estimated by calibrating chick bill, tarsus, and mid-toe + claw lengths against those of chicks for which hatching dates were known (Chapter 3). The first known chick hatched on the 12 August. The burrow in which the last egg was laid for the 1994 season failed during incubation due to kiore predation (Chapter 4), so in order to determine the period over which chicks would have hatched in the absence of kiore, the latest hatching date was estimated by adding the mean incubation period to the date when this egg was laid. The latest hatching date was, therefore, estimated to be 17 October (Figure 2.2). Eggs were hatched successfully at nine (35%) of the 26 nests monitored throughout the incubation period. The causes and timing of incubation failure are presented in Chapter Four.

Of the 17 nests where incubation failed, one or both members of 11 pairs were found on one or more occasions in their burrows after the failure. The total number of times failed breeders were found in burrows, and the time of day that they were found is shown in Table 2.3.

Table 2.3: Visits by Little Shearwater adults to burrows after breeding failure. For some burrows where adults returned there was more than one visit, thus there were 19 visits to 11 burrows.

	single birds	pairs of birds
Present during day	2	7
Present only at night	8	2

Pairs of failed breeders were more likely to remain in burrows during the day than single birds ($\chi^2_c = 4.23$, 1*df*, $P < 0.05$). In all but one case each pair of birds had been incubating an egg together before failure. One pair comprised two birds which had both incubated in separate nests. This pair had also been found together in the pre-laying period, and may have had one or more extra-pair copulations. The mean number of days at which Little Shearwaters visited the nest after failure was 26 ± 19.05 (range = 1 - 59, n = 19). Some nests failed while I was absent from Lady Alice Island, so the number of days after nesting failure that birds visited was calculated from the date at which I first returned to the island after nests had failed. Therefore, the mean number of days at which Little Shearwaters visited nests after failure was probably greater than that recorded. Failed burrows were not checked every day so as to avoid unnecessary damage to the surrounding vegetation and soil. There may, therefore, have been more failed breeders returning to the breeding site than were recorded. Also, failed burrows were usually checked during the day, but some birds may have visited and departed again during the night.

2.3.3 Effects of Investigator Disturbance

Of the ten control burrows monitored during the incubation period, three (30%) burrows were successful to the hatching stage. There was no difference in breeding success between the study and control burrows ($\chi^2_1 = 0.07$, n.s.), which indicates that the impact of investigator disturbance on Little Shearwater breeding success during the incubation period was minimal.

2.4 **Discussion**

The general trends in the breeding biology of the Little Shearwater during the pre-chick stage are similar to other Procellariiformes (see Warham (1990) for a review). The time at which birds first return to the breeding ground was not determined but appears to be poorly defined, which is typical of non-migratory seabirds (Warham 1990). Breeding males were found in burrows up to five weeks before mating took place. This long re-occupation period was probably used to prospect for and claim burrows, build nests, and establish pair bonds, as has been suggested for the Westland Black Petrel (*Procellaria westlandica*) (Baker & Coleman 1977).

Little Shearwater pairs were never found together in a burrow for longer than one day during the mating period, so it appears that the female needs only one short visit to ensure fertilisation (M. Imber, *pers. comm.*). The Little Shearwater has a relatively long pre-laying exodus (mean = 33 days) compared with most other Procellariiformes (see Warham 1990), although it is similar in length to some *Puffinus* species such as Buller's Shearwater *P. bulleri* (Harper 1983).

Little Shearwaters have a very long egg laying period (Figure 2.3) compared to other Procellariiformes (see Warham 1990; Table 13.1), with eggs being laid over 62 days in 1994. This asynchrony in laying may be due to the Little Shearwater being non-migratory. Procellariiformes which migrate usually exhibit synchronous egg laying so that chicks have time to fledge and adults can complete breeding duties before migration (Lack 1966). The Sooty Shearwater (*P. griseus*) and the Short-tailed Shearwater (*P. tenuirostris*), both trans-equatorial migrants, have much shorter laying periods of 12 and 14 days respectively (Serventy 1963, Warham *et. al.* 1982). Alternatively, some non-migratory species such as the Westland Black Petrel also have a synchronous laying period. Baker & Coleman (1977) suggest that because *P. westlandica* has a long incubation and chick period, synchronous laying is necessary to allow adults time to achieve breeding condition in the following season. The Little Shearwater, however, is a sedentary species with relatively short incubation and chick periods compared to other Procellariiformes. The greater time available to it during the breeding season may therefore accommodate the extended laying season. There may be less selection for synchronous laying in the Little Shearwater.

There are two contrasting hypotheses as to what influences the timing of laying in seabirds. Lack (1954) proposed that there is an optimal time for laying so that the young hatch when the food supply is at a maximum, and the chance of rearing a chick successfully is increased. Alternatively, Perrins (1970) suggested that laying dates reflect the earliest dates by which females acquire the food needed to form eggs. This view has been supported by a study of seabirds breeding in the Gulf of Alaska (Hatch & Hatch 1990). The 11 species monitored are relatively synchronous in the timing of laying, but become less synchronous as the season progresses, so the period of chick rearing would not coincide with maximum food availability for all species. The strongly asynchronous distribution of Little Shearwater laying, and therefore hatching dates, suggests that if food availability is variable during the breeding season, it does not strongly influence either the female's ability to form the egg, or the ability of a pair to raise a chick.

This view is further supported by the lack of correlation between the egg volume index and the timing of laying (Figure 2.6). A decline in egg size as the laying season progresses has been noted in several seabirds, such as gannets (*Sula bassana* (Nelson 1966)), Manx shearwaters (*P. puffinus* (Brooke 1978)), Razorbills (*Alca torda* (Lloyd 1979)), and Thick-billed Murres (*Uria lomvia* (Birkhead & Nettleship 1982)). Birkhead and Nettleship (1982) suggested that the seasonal decrease in the egg size of Thick-billed Murres is an adaptive response that minimises the delay in laying as environmental conditions decline throughout the season. As egg size of the Little Shearwater does not decrease during the laying period, this may indicate that any seasonal decline in food supply is not great enough to result in selection for a smaller egg size. Another factor affecting egg sizes in seabirds is female age, as older, more experienced females usually lay larger eggs (Brooke 1978, Weimerskirch 1990). As the ages of the birds in this study were unknown, I could not determine whether egg size was related to female age.

Little Shearwaters showed a right-skewed laying curve (Figure 2.3), with half of the eggs being laid in the first third of the laying period. Right-skewed laying is a widespread phenomenon in marine birds (Gochfield 1980, Hatch & Hatch 1990), and may be an indication of the age distribution of breeding females. For many seabirds, young females lay later than older, more experienced birds (Brooke 1978, Ryder 1980). The right-skewed laying curve of the Little Shearwater may be due to young, inexperienced females laying late in the season. Hatch and Hatch (1990) predicted that the shape of laying curves of seabird species would change over time as recruitment and the age distribution of adults varied. Alternatively, if the Little Shearwater population is below its maximum level, there would be more food available for breeding birds. Therefore, birds which would usually delay breeding, such as new breeders and birds which bred late in the previous year, may be able to lay, albeit late in the season (M. Imber, *pers. comm.*). Thus, the right-skewed distribution of laying dates may be due to the Little Shearwater population being depressed as a result of kiore predation (Chapter 4) or some other factor.

There is increasing evidence that extra-pair copulations can be common in apparently monogamous species (reviewed by Westneat *et. al.* 1990). Males of monogamous species are expected to attempt extra-pair copulations with mates of other males (Trivers 1972), which would increase their reproductive success. In the

Procellariiformes, extra-pair copulations have been reported only for the Wandering Albatross (*Diomedea exulans* (Tomkins 1983)), the Northern Fulmar (*Fulmarus glacialis* (Hatch 1987)), and the Short-tailed Shearwater (*P. tenuirostris* (Austin *et. al.* 1993)). Austin *et. al.* (1993) suggested that because Short-tailed Shearwaters have a low mean reproductive output, any male that secures an extra-pair copulation can increase his fecundity, and may also increase his survival rate by not breeding himself. Furthermore, females may benefit from extra-pair copulations by insuring against infertile mates. Circumstantial evidence, such as partner and burrow swapping, suggests that Little Shearwaters also engage in extra-pair copulations, and, if so, these benefits would also apply.

The length of the incubation period of the Little Shearwater (mean = 55 days) is similar to other *Puffinus* species (Warham 1990, Table 14.2). Males spent a longer time incubating than females (Table 2.1), which is unusual for Procellariiformes as both sexes usually share incubation equally (Warham 1990). Longer incubation by the male may compensate for the energetic investment by the female in producing the egg (Simons 1985). However, due to the small number of birds for which total incubation shifts were recorded, care must be taken in interpreting these results.

For birds not to lose weight during the total incubation period, weight gained while feeding at sea during an "off duty" period must equal weight lost during incubation (Brooke 1978). In the Little Shearwater, mean weights of each sex at the start of a new shift remained relatively stable (Figure 2.7) indicating that while feeding at sea, adults replaced weight lost during incubation.

Temporary absence from the nest is common in Procellariiformes (Boersma & Wheelwright 1979, Johnstone & Davis 1990), in which the embryo can survive intermittant chilling (Matthews 1954). The length of time spent away from the nest depends on a bird's ability to restore reserves at sea (Chaurand & Weimerskirch 1994), and most often occurs when the mate at sea does not return before the reserves of the incubating bird are depleted (Johnstone & Davis 1990). In the Little Shearwater, there was no difference between the weights of birds when relieved and the weights of those which left eggs unattended. This indicates that Little Shearwaters reach a critical low mass during incubation, after which, if they are not relieved, they must leave the egg unattended and return to sea to feed. This is supported by birds which had reached a low weight and left eggs unattended for one or two days, then returned at an increased mass. Chaurand and Weimerskirch (1994) found that Blue Petrels (*Halobaena caerulea*) left eggs unattended more at mid-incubation, and related this to a decrease in food availability at this time. As there was no difference in the proportion of Little Shearwater eggs left unattended during each week after laying (Table 2.2), it would appear that food availability does not vary greatly during incubation. Intermittent incubation can result in an increased incubation period (Matthews 1954, Imber 1976, Boersma & Wheelwright 1979, Johnstone & Davis 1990), and a decrease in breeding success (Boersma & Wheelwright 1979, Chaurand & Weimerskirch 1994). Due to the high proportion (55%, n = 29) of nests which failed during incubation, primarily as a result of kiore predation (Chapter 4), I could not determine whether intermittent incubation influenced either the length of the incubation period or breeding success. Little Shearwater embryos can resist periods of chilling of up to seven days, at least late in the incubation stage, and still hatch, so prolonged unattendance does not necessarily result in hatching failure. For birds suspected to have deserted the nest, the mean weight at desertion (248 ± 25.2g, n = 3) was much higher than that of birds relieved by their partner (197 ± 19.2g, n = 15). This indicates that birds which deserted did not do so due to a depletion of body reserves. Egg desertion is widespread in the Procellariiformes, and is usually caused by a bird's mate failing to relieve it of incubation duty (Warham 1990). However, as the Little Shearwaters suspected of desertion left the nest early in an incubation shift and at a high body mass, this may indicate that these birds were inexperienced breeders (Coulson & White 1958).

Attendance at the nest site after breeding failure may be to re-establish pair bonds for the following season. This is supported by the number of breeding pairs which remained in burrows during the day rather than only staying for a night (Table 2.3). The lack of single birds in burrows during the day may have been due to birds waiting in burrows for mates at night, then returning to sea before dawn when their mates did not also return to the burrow.

2.5 **References**

Austin, J.J.; Carter, R.E.; Parkin, D.T. 1993. Genetic evidence for extra-pair fertilisations in socially monogamous Short-tailed Shearwaters, *Puffinus tenuirostris* (Procellariiformes: Procellariidae), using DNA fingerprinting. Australian Journal of Zoology 41: 1-11.

Baker, A.J.; Coleman, J.D. 1977. The breeding cycle of the Westland Black Petrel: *Procellaria westlandica*. Notornis 24: 211-231.

Birkhead, T.R.; Nettleship, D.N. 1981. Reproductive biology of Thick-billed Murres (*Uria lomvia*): an inter-colony comparison. Auk 98: 258-269.

Birkhead, T.R.; Nettleship, D.N. 1982. The adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia.* Ecology 63: 300-306.

Boersma, P.D.; Wheelwright, N.T. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-petrel. Condor 81: 157-165.

Brooke, M. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx shearwater, *Puffinus puffinus*. Journal of Animal Ecology 47: 477-495.

Cameron, E.K. 1984. Vascular plants of the three largest Chickens (Marotere) Islands: Lady Alice, Whatupuke, Coppermine: north-east New Zealand. Tane 30: 53-75.

Chaurand, T.; Weimerskirch, H. 1994. Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. Ibis 136: 285-290.

Coulson, J.C.; White, E. 1958. The effect of age on the breeding biology of the Kittiwake *Rissa tridactyla*. Ibis 100: 40-51.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20: 115-120.

Glauert, L. 1946. The Little Shearwater's Year. Emu 46: 187-192.

Gochfield, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pages 207-270 *in* Burger, J.; Olla, B.L.; Winn, H.E. (eds.) Behaviour in marine animals. Vol. 4. Marine birds. New York: Plenum Press.

Harper, P.C. 1983. Biology of the Buller's Shearwater (*Puffinus bulleri*) at the Poor Knight's Islands, New Zealand. Notornis 30: 299-318.

Hatch, S.A. 1987. Copulation and mate guarding in the Northern Fulmar. Auk 104: 450-461.

Hatch, S.A.; Hatch, M.A. 1990. Breeding seasons of oceanic birds in a subarctic colony. Canadian Journal of Zoology 68: 1664-1679.

Imber, M.J. 1976. Breeding biology of the Grey-faced Petrel *Pterodroma macroptera gouldi*. Ibis 118: 51-64.

Jane, G.; Beever, R.E. 1965. A list of the vascular plants of Motu Muka (Hen and Chickens Group). Tane 11: 87-91.

Johnstone, R.M.; Davis, L.S. 1990. Incubation routines and foraging-trip regulation in the Grey-faced Petrel *Pterodroma macroptera gouldi*. Ibis 132: 14-20.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press: Oxford.

Lack, D. 1966. Population studies of birds. Oxford University Press: London.

Lloyd, C.S. 1979. Factors affecting breeding of Razorbills *Alca torda* on Skokholm. Ibis 121: 165-176.

Matthews, G.V.T. 1954. Some aspects of incubation in the Manx shearwater *Procellaria puffinus*, with particular reference to chilling resistance in the embryo. Ibis 96: 434-440.

McCallum, J.; Bellingham, P.J.; Hay, J.R.; Hitchmough, R.A. 1984. The birds of the Chickens Islands, northern New Zealand. Tane 30: 105-124.

Nelson, J.B. 1966. The breeding biology of the gannet *Sula bassana* on the Bass Rock, Scotland. Ibis 108: 584-626.

Percy, C.A. 1955. A primary study of the vegetation of Marotiri Island. Tane 7: 3-6.

Perrins, C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Perrins, C.M.; Brooke, M. 1976. Manx Shearwaters in the Bay of Biscay. Bird Study 23: 295-300.

Ryder, J.P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. Pages 153-168 *in* Burger, J.; Olla, B.L.; Winn, H.E. (eds.) Behaviour of marine animals. Vol. 4. Marine birds. New York: Plenum Press.

Serventy, D.L. 1956. A method for sexing petrels in field observations. Emu 56: 213-215.

Serventy, D.L. 1963. Egg-laying timetable of the Slender-billed Shearwater *Puffinus tenuirostris*.

Simons, T.R. 1985. Biology and behaviour of the endangered Hawaiian Dark-rumped Petrel. Condor 87: 229-245.

Skegg, P.D.G. 1964. Birds of the Hen and Chickens Islands. Notornis 11: 159-182.

Tomkins, R.J. 1983. Fertilisation of Wandering Albatross eggs on Macquarie Island. Notornis 30: 244-246.

Trivers, R.L. 1972. Parental investment and sexual selection. Pages 136-179 *in* Campbell, B. (ed.) Sexual selection and the descent of man. Baltimore: Williams & Williams.

Turbott, E.G. 1990. Checklist of the Birds of New Zealand. Random Century In association with the Ornithological Society of New Zealand.

Warham, J. 1990. The petrels, their ecology and breeding systems. Academic Press: London.

Warham, J.; Wilson, G.J.; Keeley, B.R. 1982. The annual cycle of the Sooty Shearwater *Puffinus griseus* at the Snares Islands, New Zealand. Notornis 29: 269-292.

Weimerskirch, H. 1990. Weight loss of Antarctic Fulmars *Fulmarus glacialoides* during incubation and chick brooding. Ibis 132: 68-77.

Westneat, D.F.; Sherman, P.W.; Morton, M.L. 1990. The ecology and evolution of extra-pair copulations in birds. Pages 331-369 *in* Power, D.M. (ed.) Current Ornithology. Vol. 7. New York: Plenum Press.

Chapter Three: The Chick Rearing Stage of the Little Shearwater

3.1 Introduction

Shearwaters, like all other Procellariiformes, have a long chick rearing period relative to their body size. Chicks are semi-precocial, becoming homoeothermic soon after hatching, which allows adults to make extended feeding trips (Ricklefs 1979). Both parents are needed to raise a chick. Each adult can deliver, at most, one meal every 24 hours, and often less frequently than this depending on the distance to the feeding ground. Records of a single adult rearing a chick to fledging are very rare (Warham 1990). Each adult generally contributes equally to food provisioning to the chick.

All Procellariiformes accumulate large quantities of fat during the nestling period (Warham 1990). Lack (1968) suggested this characteristic provides insurance against poor feeding conditions. Food resources of pelagic seabirds are generally believed to be patchy and unpredictable (Ashmole 1971). More recent studies of procellariiform breeding ecology, however, have questioned Lack's theory, due to lack of evidence of either chicks starving as a result of poor feeding conditions, or significant variation in the provisioning rates of adults (Ricklefs *et. al* 1985, Hamer & Hill 1993).

During this study, I obtained data on the chick rearing stage of the North Island Little Shearwater (*Puffinus assimilis haurakiensis*), which breeds on islands off the north-east coast of the North Island of New Zealand. Very little is known about chick rearing in the Little Shearwater. Basic data have been published for the West Australian Little Shearwater *P. a. tunneyi* . Glauert (1946) recorded that the chicks of *P. a. tunneyi* are fed every second night by both parents for the first two weeks after hatching, then one or two times every five nights thereafter until a fasting period of about 10 days before fledging. Warham (1955), however, reported that the chicks of *P. a. tunneyi* are visited by usually one and often both parents each night.

In this chapter, I present details of chick hatching, growth rates, and fledging. I also describe the behaviour of adults during the chick rearing period, and discuss the role of fat accumulation in chicks in relation to adult provisioning rates and chick mass. Finally, I present details of a food provisioning strategy previously undescribed in Procellariiformes, by which adults coordinate feeding shifts, and discuss this strategy in relation to chick development.

3.2 **Methods**

3.2.1. Study site

Lady Alice Island (138 ha, 35°54'S, 174°44'E), is the largest of the Chickens Islands in the Hen and Chickens Group. Access to all of the islands in this group is restricted. Although Lady Alice Island has been modified in the past by Maori occupation, cattle grazing and fires (Percy 1955), it currently supports a diverse flora (Percy 1955, Jane & Beever 1965, Cameron 1984). The valleys follow a transition from flax (*Phormium tenax*) and coastal scrub in the lower reaches through kohekohe (*Dysoxylum spectabile*) - puriri (*Vitex lucens*) forest to pohutukawa (*Metrosideros excelsa*) - puriri forest at the heads of the valleys. Ridges are dominated by kanuka (*Kunzea ericoides*) (Percy 1955). Bird surveys on Lady Alice Island have been conducted by (Skegg 1964) and McCallum *et al* (1984). Four species of procellariid seabirds breed on Lady Alice Island - Little Shearwaters and Grey-faced Petrels (*Pterodroma macroptera*) in the winter; and Pycroft's Petrels (*P. pycrofti*) and Flesh-footed Shearwaters (*Puffinus carneipes*) in the summer. Tuatara (*Sphenodon punctatus*) are present in densities near the lower limit of the range observed on rat-free islands (Crook 1973). Kiore were present on Lady Alice Island until 27 October, 1994, when they were eradicated by an aerial poison drop. It is not known how long kiore had been on this island (R. J. Pierce, *pers. comm.*)

3.2.2 Chick hatching and growth

Four trips were made to the study site during the chick rearing period; 16 - 30 August, 12 - 30 September, 12 - 21 October, and 18 November - 4 December 1994. Thirteen burrows containing Little Shearwater chicks were monitored during the chick rearing period. All of these burrows were within one of four sites on Lady Alice Island (Figure 3.1).

Hatching dates and adult brooding behaviour after hatching were recorded for chicks which hatched while I was at the study site. For chicks whose date of hatching was unknown, age was estimated by calibrating the culmen length when the chick was first found against the growth of the culmen of known-age chicks. The following measurements were taken approximately every six days using vernier calipers accurate to ± 0.1mm: culmen length; tarsus length; mid-toe + claw length; and tail length. The unflattened wing length was measured to the nearest mm using a flanged ruler. To determine the rate of mass increase, chicks were weighed at the same time each morning using a Pesola spring balance accurate to ± 1g.

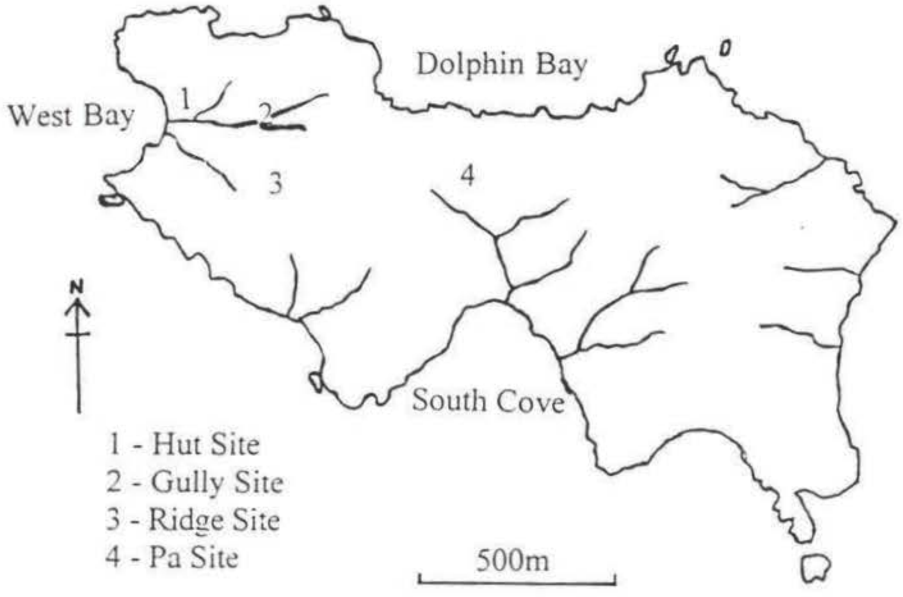


Figure 3.1: Location of study sites on Lady Alice Island.

3.2.2 Adult Behaviour

Adult visitation during the chick rearing period was monitored at five burrows. These burrows were checked nightly, and the parent feeding the chick was recorded. Shearwaters breeding in these burrows had been banded for individual identification and sexed during the incubation period (Chapter 2).

At the eight other burrows, adult visitation was not monitored. Feeding frequency was determined by weighing chicks each evening before the adult returned, and subtracting this mass from the mass the following morning. Chicks which had a positive mass increase overnight were assumed to have been fed during the night.

Data are given as the mean ± 1SD.

3.3 **Results**

3.3.1. Chick hatching and growth

The hatching date was recorded for three chicks. The ages of nine chicks were estimated by calibrating bill, mid toe + claw, and tarsus lengths when the birds were first found against growth measures of chicks of known age. A further chick was found in a new burrow just prior to fledging, and the age of this chick was not determined.

The timing of events during the chick rearing period is shown in Figure 3.2. The first known chick hatched on the 12 August. The burrow in which the last egg was laid for the 1994 season failed during incubation due to kiore predation (Chapter 4), so in order to determine the period over which chicks would have hatched in the absence of kiore, the latest hatching date was estimated by adding the mean incubation period to the date when this egg was laid (Chapter 2). The latest hatching date was, therefore, estimated to be 17 October.

Figure 3.2: Timing of Little Shearwater breeding activity during the chick rearing period. * denotes that date was estimated.

Chicks were brooded at all of the burrows where I was present at the time of hatching (n = 3). The total number of days between chick hatching and the end of the brooding period was recorded at two burrows. One chick was brooded for two nights up to four days old, and the other chick was brooded for three nights up to five days old.

Chick mass in relation to age is shown in Figure 3.3. The mean chick weight at hatching was 31 ± 0.5g (n = 3). Chick mass increased at a mean rate of 5.8g/day until the mean maximum weight of 283 ± 21.4g (range = 267 - 320, n = 5) was reached at approximately 45 - 46 days of age. The mean maximum chicks mass was 128% of the mean adult mass of 221 ± 3.1g during the pre-laying period (Chapter 2). After this age, the mass of individual chicks became more variable and ranged between 205g and 342g (n = 9) until 61 days old. The maximum mass of 342g is 155% of the mean adult mass during the pre-laying period. After about day 61, chick mass tended to decrease until fledging. Weights at fledging were variable, with a mean weight of 233 ± 17.1g (range = 205 - 257, n = 5), which was equal to 105% of the mean adult weight during the pre-laying period. The mean age at fledging was 73 ± 3.0 days (range = 69 - 77, n = 4). Fledging occured from 24 October in 1994. The latest fledging date was estimated by adding the mean age at fledging to the latest hatching date (see above). The date at which the last chick would have fledged, had it survived, was therefore estimated to be 10 January 1995.

The rates of growth for the bill, mid toe + claw, tarsus and wing of chicks are shown in Figure 3.4. Bill length increased throughout the chick growth period, while mid toe + claw and tarsus lengths increased rapidly to about 35 days old then slowed.

The rate of wing growth was slow to approximately 20 days old, then increased as the primaries started to emerge.

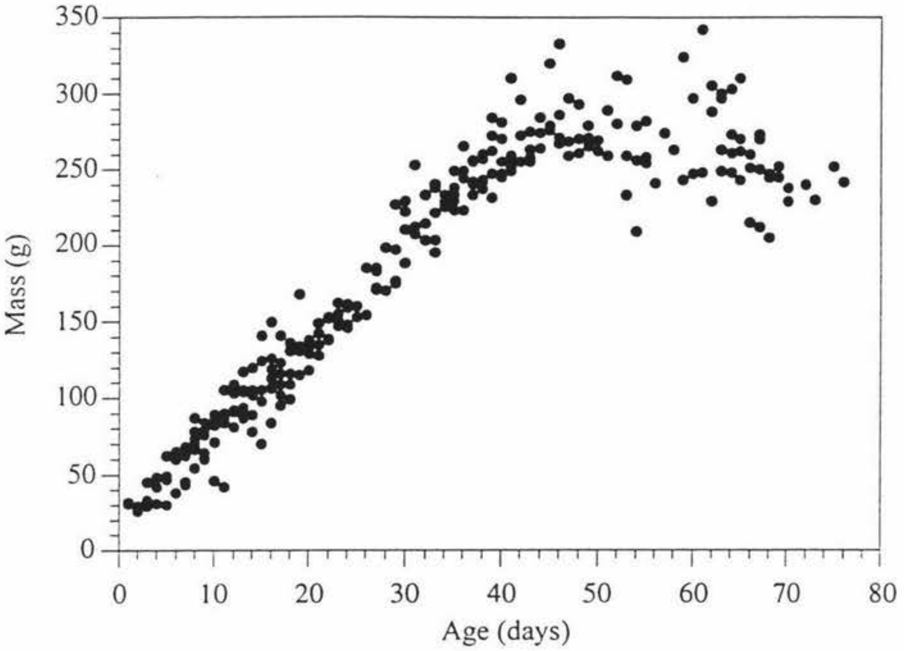


Figure 3.3: Mass of Little Shearwater chicks in relation to age. (n= 12).

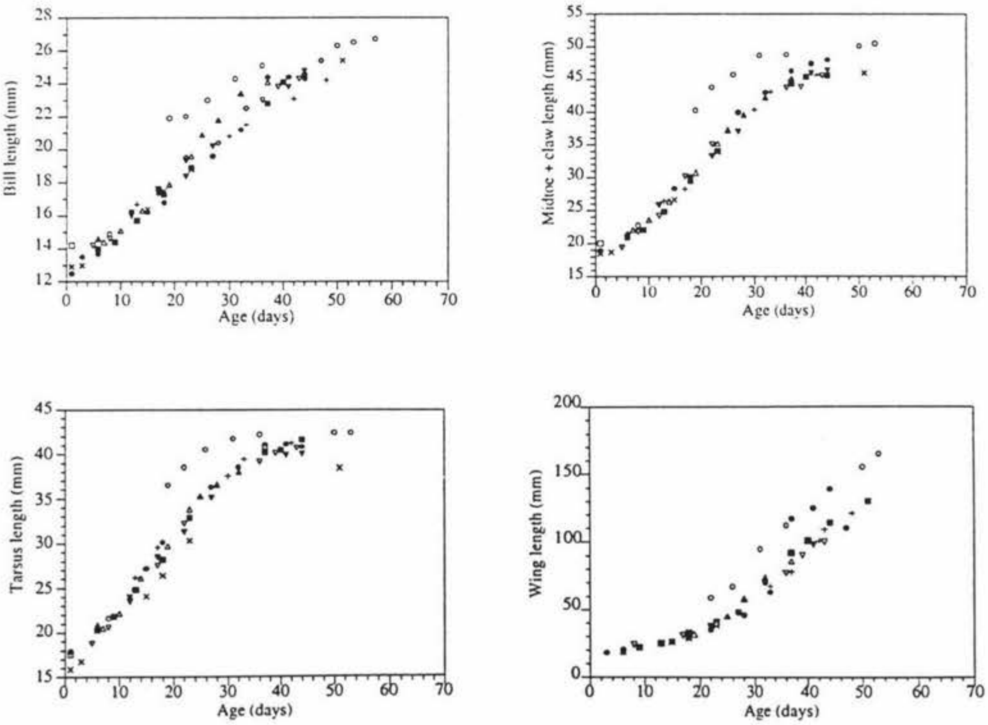


Figure 3.4: Rates of growth of the bill, mid toe + claw, tarsus and wing of Little Shearwater chicks. (n = 12).

3.3.2 Adult feeding behaviour

At the five burrows where visits by individual parents were monitored, the typical pattern of chick feeding was for adults to coordinate feeding periods, with one adult feeding the chick at a time, and adults alternating feeding visits. These visits lasted 7 ± 1.6 nights (n = 9), with one adult usually continuing to feed the chick nightly until its partner returned. Chicks were fed on 96 ± 5.5% of the nights that these burrows were monitored for adult visitation (n = 93 observations). Occasionally, both adults were found feeding the chick on the same night. This occurred when one parent was at the end of it's feeding period, and the second parent had returned to resume feeding. Chicks were visited by both adults on the same night on 7% of the nights that they were fed.

At the eight burrows where adult visits were not monitored, I used the overnight weight change to determine whether chicks had been fed up to 45 days old. After this age, chick mass increase levelled out (Figure 3.3), and overnight mass changes decreased for some chicks known to have been fed during the night. I could not, therefore, use overnight mass changes to determine whether a chick had been fed after the peak mass had been gained. At these burrows, chicks showed an overnight weight increase, indicating that they had been fed, on 93% (n = 148 observations) of the days they were weighed.

Table 3.1: Comparison of methods used to determine whether Little Shearwater chicks were fed. These were: 1. monitoring burrow at night for adult visitation or 2. determining overnight weight change of chicks.

	Method of determining whether chicks were fed	
	Burrow monitored	Chick weighed
Chicks fed	89	138
Chicks not fed	4	10
TOTAL	93	148

There was no significant difference in chick feeding rates using the two methods of determining whether adults had fed chicks ($\chi^2_1 = 0.96$, n.s.) (Table 3.1). This suggests that measuring the overnight mass change of chicks is an accurate method for determining feeding frequency, at least up until the peak mass is gained. The overnight mass change and the frequency of these changes are shown in figure 3.5. If the number of adults (ie. one or two) feeding the chick in one night was directly correlated with overnight weight increase, then this figure may show a bimodal distribution of weight gain. A bimodal distribution, therefore, could be used to determine how many adults fed the chick in one night. The data do not exhibit a clear bimodal pattern, which indicates that there was no obvious difference in overnight mass increase of chicks according to whether one or two adults delivered a meal in any one night. For chicks which showed a positive overnight mass change, the mean weight increase was 21.4 ± 12.5g (range = 3 - 72, n = 189).

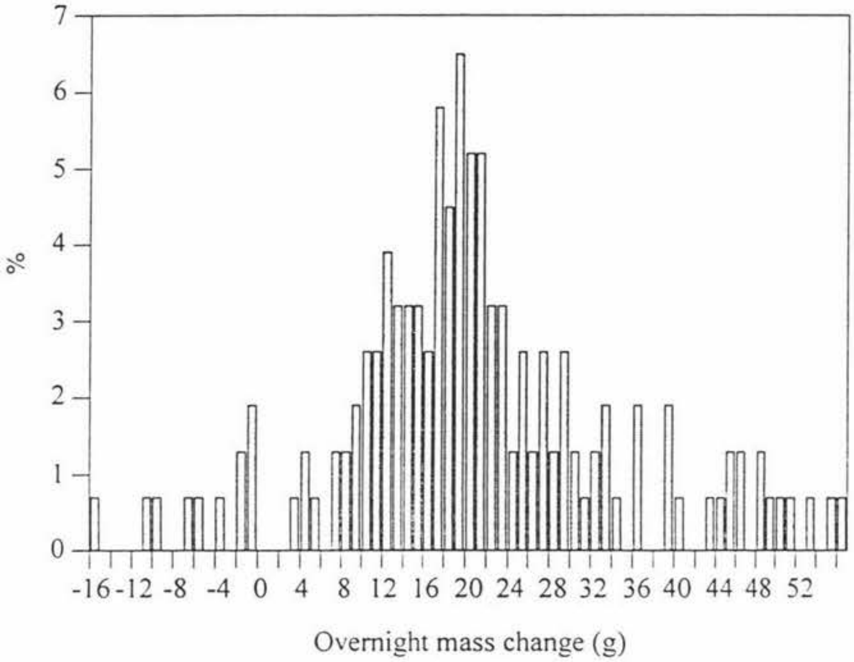


Figure 3.5: Overnight mass change of Little Shearwater chicks. (n = 12).

The overnight weight increase of chicks in relation to age is shown in Figure 3.6. Due to the lack of independence in the data, I could not determine whether the change in weight increase was significant. However, as the slope of the regression line is positive, this suggests that the overnight increase in weight gets larger as chicks get older, and indicates that meals delivered to chicks increase with the age of the chick.

The proportion of nights that chicks were fed in relation to their age is shown in Figure 3.7. Chicks appeared to be fed at approximately the same rate up to 45 days old. After this age, I did not use overnight mass change to determine whether chicks had been fed (see above), and feeding frequency was recorded for only one chick, for which I recorded visits by its parents to the burrow.

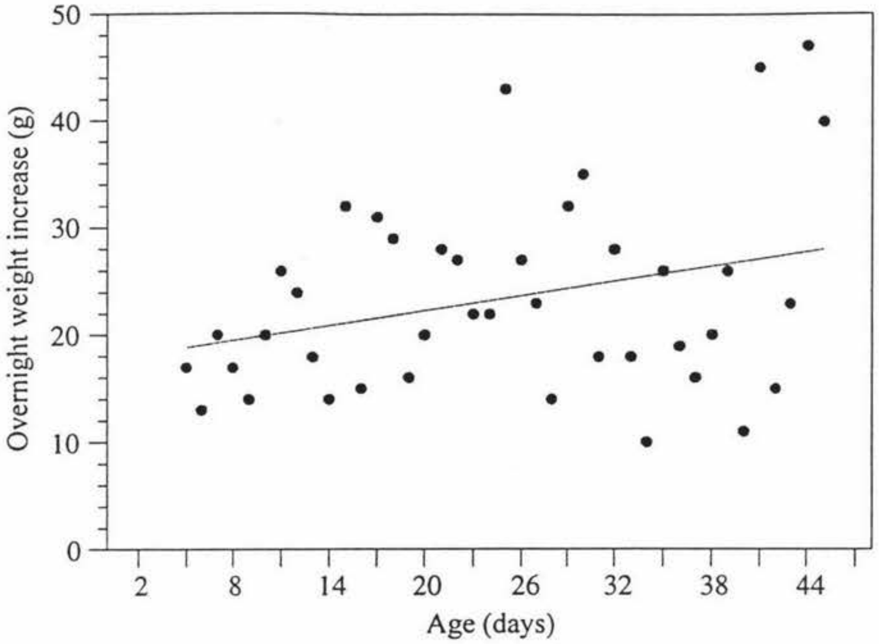


Figure 3.6: Overnight weight increase of Little Shearwater chicks in relation to age. (n = 12, R = 0.3).

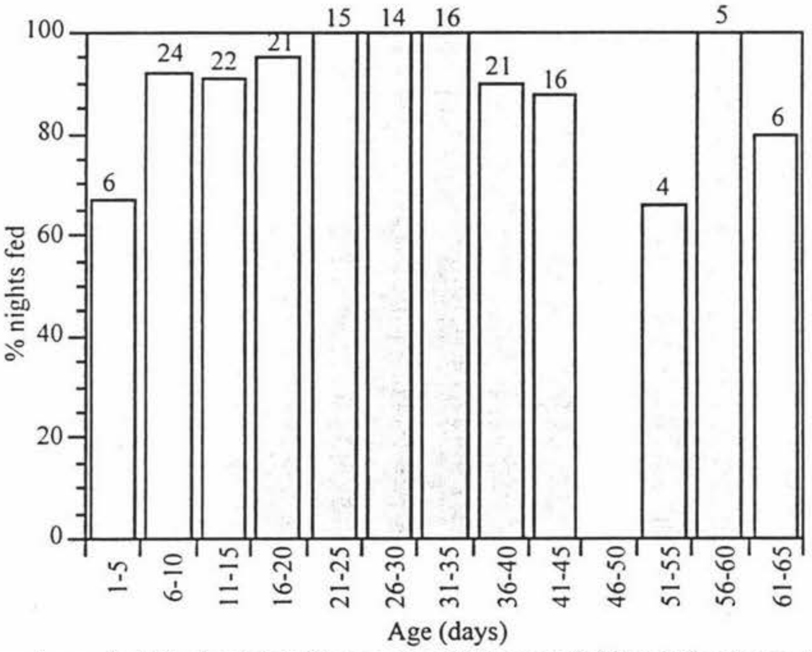


Figure 3.7: Percentage of nights that Little Shearwater chicks were fed in relation to age. The number of observations for each age class is shown at the top of each column.

3.3.3 Effect of investigator disturbance

In order to determine whether handling adults had an effect on food delivery to chicks, I tested for a difference between the overnight mass change of chicks whose parents were handled, and those whose parents were not interacted with during the study. Chicks whose parents were not handled showed a greater overnight mass increase ($t = 2.16$, $p < 0.05$, $df = 5$), indicating that handling adults during the chick rearing period may result in parents delivering less food to the chick.

3.4 **Discussion**

Hatching occured over a long period relative to other Procellariidae (Figure 3.2), and may have been influenced by the Little Shearwater being non-migratory, and also possibly by a lack of variation in food availability during the breeding season (see Chapter 2).

Chicks were brooded for only a short time after hatching, which may indicate that chicks quickly attain adult body temperature, as in Bonin Petrel (*Pterodroma hypoleuca*) chicks (Pettit *et. al.* 1982). A guard period of 2 - 3 days is common with burrow nesting Procellariidae (Warham 1990), although this can vary greatly between species and individual birds.

Little Shearwater chicks achieved pre-fledging weights well above the mean adult mass (Figure 3.3). This is typical of procellariiform chicks, in which the accumulation of large deposits of lipid reserves is followed by a pre-fledging weight loss (Warham 1990). These characteristics, along with slow development and a long fledging period, were suggested by Lack (1968) and Ashmole (1971) as being adaptations to meagre, distant, or fluctuating food resources. However, during this study I noted two aspects of the chick rearing behaviour of the Little Shearwater which were not compatible with this theory.

Firstly, up until 45 days of age, a mean of 96% of Little Shearwater chicks were fed on each night that burrows were monitored. Frequent feeding of chicks does not support the theory that large fat deposits in the Procellariiformes are an adaptation to poor feeding conditions, when the frequency of meals delivered to the chick may decrease. During his study of the Little Shearwater on Selvagem Grande in the North Atlantic Ocean, Hamer (1994) had very similar results, with an average of 95% of chicks being fed each night. Other studies have also found that intervals between meals are rarely longer than a few days (Harris 1966, Ricklefs *et. al.* 1985, Hamer, 1993). Furthermore, studies of meal delivery to Leach's Storm-petrel (*Oceanodroma leucorhoa*) (Ricklefs *et. al.* 1985) and Wilson's Storm-petrel (*Oceanites oceanicus*) (Croxall *et. al.* 1988) have found no evidence of poor feeding conditions that substantially deplete chick fat reserves. Feeding rates of chicks may be reduced during periods of bad weather, although it is unlikely that such conditions would be sufficiently regular and widespread to result in selection for large fat deposits in

Procellariiformes (Hamer 1994). The results of this study do not discount the possibility that the rate of chick feeding may differ between breeding seasons. Chick provisioning, therefore, should be monitored for several years in order to confirm the regularity of chick feeding in the Little Shearwater.

Secondly, there were no obvious differences in the proportion of nights that Little Shearwater chicks were fed in relation to their age (Figure 3.7). This observation further contradicts the theory that large fat deposits are an adaptation to an unpredictable food supply, as chicks were fed regularly, at least until 45 days old. Other studies have also found that feeding rate is not adjusted to the age of chicks (Harris 1966, Ricklefs *et. al.* 1985, Hamer & Hill 1993, Hamer 1994).

Ricklefs (1983) questioned Lack's (1968) theory of energy limitation during breeding in Procellariiformes, and suggested that the reproductive output of seabirds is limited by problems associated with transporting food over long distances rather than by the foraging ability of adults. Using a simulation model based on food provisioning and physiological measurements of Leach's Storm-petrels, Ricklefs and Schew (1994) concluded that large fat reserves were a result of parents overfeeding chicks on average in order to minimise the probability that chicks will starve by chance. They suggested that this strategy was insurance against stochastic variation in food provisioning by individual birds rather than variation in food availability. Ricklefs and Schew's (1994) theory has since been refuted by Bolton (1995). During his study of British Storm-petrels (*Hydrobates pelagicus*), Bolton found that adults modified their provisioning effort in response to the nutritional status of chicks. His results indicate that food delivery rates for this species are not significantly influenced by stochasticity in either feeding success or food delivery, as parents regulated the amount of food delivered to chicks. Regulation of food delivery would not be predicted if either resource availability or food provisioning ability were unpredictable. If this was so, adults would be expected to increase food provisioning up to the maximum amount they are able to deliver (Bolton 1995).

Bolton's results are in contrast to other studies, in which adults have not responded to changes in food requirements of chicks resulting from manipulation of food demands at the nest (Ricklefs *et. al.* 1985, Ricklefs 1987, Ricklefs 1992, Hamer & Hill 1994). Ricklefs (1992) concluded that solicitation behaviour by the chick 'either does not convey information about nutritional status, or parents do not or cannot act upon that information'. In this study, I was not able to determine whether the rate of food provisioning in the Little Shearwater was related to the nutritional status of chicks, because the size of meals delivered to chicks was not determined. Overnight weight increase underestimates meal size due to mass loss before and after feeding (Harper 1976, Warham 1990, Hamer 1994), so these data could not be used to determine meal size. Nevertheless, there was a general trend for overnight changes in chick mass to increase with age, although its significance could not be tested (Figure 3.6). This indicates that Little Shearwater adults may adjust meal size according to chick age. Alternatively, it may be that chicks are able to accept larger meals as they grow, rather than adults delivering larger meals.

This study presents the first known record of Procellariiformes coordinating feeding visits to the chick, rather than delivering food independently of their partner. The typical chick feeding strategy in the Little Shearwater was for adults to alternate feeding shifts. One parent would, therefore, feed the chick for approximately seven nights in a row, after which this bird would finish feeding and the other parent would return to resume feeding for about the same period of time. This contrasts with Hamer's (1994) study of the Little Shearwater, in which each bird fed the chick independently of its partner. Coordination by parents during chick rearing would be more likely if the food supply was steady. If the food supply was patchy and unpredictable, adults might have to adopt an independent foraging strategy, as the time taken to obtain each meal for the chick could not be anticipated. In this situation, the best strategy could be to feed the chick as often as possible, regardless of the frequency of food delivery by the other parent. Independent foraging by parents during chick rearing is a common strategy in Procellariiformes (Ricklefs *et. al.* 1985, Chaurand & Weimerskirch 1994), and partially supports the hypothesis that fat deposits are an adaptation to stochastic variation in food supply to chicks (Ricklefs & Schew 1994). If parents feed the chick independently of one another, the chick could be left unfed for longer periods than usual due to chance variation in food delivery. In this study, however, there was little possibility that chicks would be left unfed for long periods because the parents coordinated their feeding effort. This observation refutes Ricklefs and Schew's (1994) theory that large fat deposits are insurance against stochastic variation in food provisioning by individual birds.

An alternative hypothesis for fat reserves in Procellariiformes is that chicks accumulate fat early in the growth period, when energy requirement is low, to offset higher metabolic requirements later in development (Ricklefs 1990). It has also been suggested that parents oversupply their chicks with energy in order to achieve an adequate supply of nutrients such as calcium (Taylor & Konarzewski 1992). Further investigation of the factors influencing fat accumulation in Little Shearwaters is required to determine the role of this characteristic.

Independent foraging may prevent parents from obtaining reliable information about the chick's food requirements at the next visit to the nest, resulting in an intrinsic feeding rhythm by parents (Bolton 1995). As feeding visits by Little Shearwater adults to the chick are coordinated, it may be possible that parents can assess the nutritional status of the chick during each feeding shift more accurately than species which forage independently, and are able to regulate food delivery accordingly. However, in order to determine unequivocally whether Little Shearwater adults are regulating food delivery, experimental evidence, such as that obtained by Bolton (1995) during his study of British Storm-petrels, is required. I suggest that for species which regulate food delivery to the chick, and therefore do not feed the chick at the maximum rate, the percentage of body mass lost by chicks between obtaining the maximum body mass and fledging may be lower than for species which are fed at the maximum rate throughout the nestling period. This could result from chicks accumulating less fat relative to their body size. Using the mean maximum weight of chicks (283 ± 21.4g, n = 5) and the mean weight at fledging (233 ± 17.1, n = 5), I calculated that Little Shearwater chicks lost, on average, 17.7% of their body weight between reaching maximum mass and fledging. In order to compare this rate of weight loss to closely related Procellariiformes, I used data from Warham (1990; Table 15.4) to calculate the proportion of weight lost between maximum mass gain and fledging for 11 species in the Family Procellariidae. For these species, the mean proportion of weight loss was 25.7 ± 5.9%. Small sample sizes prevent a rigorous test of the difference between the data sets. However, as the proportion of weight loss of Little Shearwater chicks was greater than one standard deviation from the mean proportion of weight loss of the other Procellariidae, this indicates that Little Shearwater chicks lose significantly less weight prior to fledging than other members of this family. This result partially supports the hypothesis that Little Shearwater parents regulate chick feeding, and therefore do not feed chicks at the maximum possible rate. Further investigation of the proportion of weight lost from year to year is needed to discount the possibility that this result is due to some other factor. Food availability during the breeding season may have accounted for this result. If there was a reduction in the food supply during the 1994 season, chicks may have reached a lower maximum mass than that obtained during a year of plentiful food, and therefore the proportion of weight lost by chicks before fledging would have been relatively low.

There is little information on the behaviour of individual adults during chick rearing (but see Schaffner 1990, Chaurand & Weimerskirch 1994, Weimerskirch *et. al.* 1994). The effort required to assess the strategies of individual parents is considerable, therefore most studies of the chick rearing behaviour of seabirds have used the average feeding frequency of the chick by the two parents. During their study of Blue Petrels (*Halobaena caerulea*), Chaurand & Weimerskirch (1994) found that adults alternate long and short trips to sea during chick rearing. They used dietary analysis to determine the area in which adults had been feeding, and found that during long trips birds were foraging further out to sea than during short trips. They assumed that long trips provided a higher energetic yield than short trips, and that birds benefitted from these long trips by storing energy which was later utilised during short foraging trips when there was an increased frequency of chick feedings. I did not analyse the composition of meals delivered by Little Shearwater adults and therefore could not estimate where they had been feeding during the chick rearing period. Adults had, however, alternate periods of approximately one week during which they were not delivering meals to the chick. This could indicate that they were foraging further afield during these periods than when they were feeding the chick. Chaurand and Weimerskirch (1994) suggested that such a strategy could increase the energetic yield of a foraging trip in two ways. Firstly, assuming that prey patches are randomly distributed and the location of patches is unpredictable, the amount of prey encountered would be proportional to the distance travelled. Secondly, by travelling further from the breeding site, competition with conspecifics would be decreased. Little Shearwaters may be using a similar chick feeding strategy to that suggested for the Blue Petrel, that is, using shifts away from the breeding site to replenish energy supplies depleted during a chick feeding shift. It is unlikely that this strategy would be possible if Little Shearwater parents did not coordinate foraging shifts. As mentioned above, coordination reduces the variance in food delivery to the chick. Another advantage of coordinating foraging shifts is that this could allow parents to make extended trips away from the breeding site, while still maintaining a regular food supply to the chick.

The difference in overnight mass increase of chicks whose parents were handled and those whose parents were not interacted with suggests that investigator disturbance of Little Shearwater adults may have an influence on the amount of food delivered to chicks. The difference between the two groups of chicks, however, was slight, and did not appear to influence fledging success. Disturbance by researchers should be minimised, and the short- and long-term effects of research should be investigated as part of the study (Fraser 1994).

3.5 **References**

Ashmole, N.P. 1971. Seabird ecology and the marine environment. Pages 224-286 *in* Farner, D.S.; King, J.R.; Parkes, K.C. (eds.) Avian Biology. New York and London: Academic Press.

Bolton, M. 1995. Experimental evidence for regulation of food delivery to storm petrel, *Hydrobates pelagicus*, nestlings: the role of chick body condition. Animal Behaviour 50: 231-236.

Cameron, E.K. 1984. Vascular plants of the three largest Chickens (Marotere) Islands: Lady Alice, Whatupuke, Coppermine: North-east New Zealand. Tane 30: 53-75.

Chaurand, T.; Weimerskirch, H. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea* : a previosly undescribed strategy of food provisioning in a pelagic seabird. Journal of Animal Ecology 63: 275-282.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20: 115-120.

Croxall, J.P.; Hill, H.J.; Lidstone-Scott, R.; O'Connell, M.J.; Prince, P.A. 1988. Food and feeding ecology of Wilson's storm-petrel *Oceanites oceanicus* at South Georgia. Journal of Zoology 216: 83-102.

Fraser, W.R. 1994. Workshop on researcher-seabird interactions. Joint Oceanographic Institutions Inc., Washington D.C.

Glauert, L. 1946. The Little Shearwater's Year. Emu 46: 187-192.

Hamer, K.C. 1994. Variability and stochasticity of meal size and feeding frequency in the Little Shearwater *Puffinus assimilis*. Ibis 136: 271-278.

Hamer, K.C.; Hill, J.K. 1993. Variation and regulation of meal size and feeding frequency in Cory's shearwater, *Calonectris diomedea*. Journal of Animal Ecology 62: 441-450.

Hamer, K.C.; Hill, J.K. 1994. The regulation of food delivery to nestling Cory's Shearwaters *Calonectris diomedea*: the roles of parents and offspring. Journal of Avian Biology 25: 198-204.

Harper, P.C. 1976. Breeding biology of the fairy prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. New Zealand Journal of Zoology 3: 351-371.

Harris, M.P. 1966. Breeding biology of the Manx shearwater *Puffinus puffinus*. Ibis 108: 17-33.

Jane, G.; Beever, R.E. 1965. A list of the vascular plants of Motu Muka (Hen and Chickens Group). Tane 11: 87-91.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd.: London.

McCallum, J.; Bellingham, P.J.; Hay, J.R.; Hitchmough, R.A. 1984. The birds of the Chickens Islands, northern New Zealand. Tane 30: 105-124.

Percy, C.A. 1955. A primary study of the vegetation of Marotiri Island. Tane 7: 3-6.

Pettit, T.N.; Grant, G.S.; Whittow, G.C. 1982. Body temperature and growth of Bonin petrel chicks. Wilson Bulletin 94: 358-361.

Ricklefs, R.E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology 8: 84-94.

Ricklefs, R.E. 1987. Response of adult Leach's Storm-Petrels to increased foon demand at the nest. Auk 104: 750-756.

Ricklefs, R.E. 1990. Seabird life histories and the marine environment: some speculations. Colonial waterbirds 13: 1-6.

Ricklefs, R.E. 1992. The roles of parents and chick in determining feeding rates in Leach's storm-petrel. Animal Behaviour 43: 895-906.

Ricklefs, R.E.; Day, C.H.; Huntington, C.E.; Williams, J.B. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. Journal of Animal Ecology 54: 883-898.

Ricklefs, R.E.; Schew, W.A. 1994. Foraging stochasticity and lipid accumulation by nestling petrels. Functional Ecology 8: 159-170.

Schaffner, F.C. 1990. Food provisioning by white-tailed tropicbirds: effects on the development pattern of the chick. Ecology 71: 375-390.

Skegg, P.D.G. 1964. Birds of the Hen and Chickens Islands. Notornis 11: 159-182.

Taylor, J.R.E.; Konarzewski, M. 1992. Budget of elements in Little Auk (*Alle alle*) chicks. Functional Ecology 6: 137-144.

Warham, J. 1955. Observations on the Little Shearwater on the nest. Western Australian Naturalist 5: 31-39.

Warham, J. 1990. The petrels, their ecology and breeding systems. Academic Press: London.

Weimerskirch, H.; Chastel, O.; Ackermann, L.; Chaurand, T.; Cuenot-Chaillet, F.; Hindermeyer, X.; Judas, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. Animal Behaviour 47: 472-476.

Chapter Four: Little Shearwater breeding success, and evidence of predation by kiore, *Rattus exulans.*

4.1 **Introduction**

The Little Shearwater (*Puffinus assimilis*) is a member of the Procellariiformes, and is the smallest of the shearwaters. Like most species in this order, it nests in burrows and lays a one-egg clutch. There are no second clutches. The Little Shearwater is non-migratory and breeds in the winter. Five subspecies of Little Shearwater are recognised (Turbott 1990), but details of the breeding biology have been published only for the Western Australian subspecies *P. a. tunneyi* (Glauert 1946, Warham 1955, Warham 1958). For this subspecies, both members of the pair alternate incubation shifts, and the incubation period lasts for approximately 54 days.

The North Island sub-species of the Little Shearwater (*P. a. haurakiensis*) has not been assigned a conservation category (Bell 1986), and is assumed not to be threatened. A project to monitor the breeding success of the North Island Little Shearwater on Lady Alice Island was started in 1993 (R. Pierce, *unpubl.*), but due to difficulties in making regular, frequent visits to the study site, only annual productivity has been measured. In order to determine the factors affecting breeding success in a seabird, it is necessary to monitor the population throughout the breeding season so that causes of failure can be identified.

Kiore (*Rattus exulans*) are potential predators of the eggs and chicks of small seabirds (Moors & Atkinson 1984, Atkinson & Moller 1990) , and were the only introduced mammalian predator on Lady Alice Island at the time of the study. The kiore is the smallest of three rat species present in New Zealand, and is confined to offshore islands and parts of South Westland and Fiordland (Atkinson & Moller 1990). Most of the offshore islands in New Zealand with kiore are also breeding sites for burrow-nesting seabirds and, although there is little information on the impact of kiore on these New Zealand populations, they have been known to have a large impact on seabirds in other parts of the Pacific. On Kure Atoll, Hawaii, kiore prey on the eggs, chicks, or adults of at least five seabird species (Kepler 1967, Fleet 1972, Wirtz 1972). In New Zealand, there is strong circumstantial evidence that kiore prey on the eggs of the Diving Petrel (*Pelecanoides urinatrix)* (Thoresen 1967), and the eggs and chicks of Cook's Petrels (*Pterodroma cookii*) (Imber 1978, Imber 1984) .

In this chapter I present data on the breeding success and causes of breeding failure for the North Island Little Shearwater during the 1994 breeding season. As I was at the study site for the majority of the breeding season, I was able to determine the cause of failure for most of the breeding burrows monitored. I also present evidence that kiore prey on the eggs of the Little Shearwater, and discuss the significance of this impact.

4.2 **Methods**

4.2.1 Study Site

Lady Alice Island (35°54'S, 174°44'E; 138 ha), is the largest of the Chickens Islands in the Hen and Chickens Group, and is a limited access nature reserve. Although Lady Alice Island has been modified in the past by Maori occupation, cattle grazing and fires (Percy 1955), it currently supports a diverse flora (Percy 1955, Jane & Beever 1965, Cameron 1984). Four procellariid species breed on Lady Alice Island - Little Shearwaters and Grey-faced Petrels (*Pterodroma macroptera*) in the winter; and Pycroft's Petrels (*P. pycrofti*) and Flesh-footed Shearwaters (*P. carneipes*) in the summer. Kiore were present on Lady Alice Island for most of the study but were eradicated on October 27, 1994, by an aerial poison drop. It is not known how long kiore have been present on Lady Alice Island (R. J. Pierce, *pers. comm*). Tuatara (*Sphenodon punctatus*) are present in densities near the lower limit of the range observed on rat-free islands (Crook 1973).

4.2.2 Monitoring burrows for causes of failure

Six trips were made to Lady Alice Island during the 1994 Little Shearwater breeding season; 14 - 22 June, 19 - 29 July, 16 - 30 August, 12 - 30 September, 12 - 21 October, and 18 November - 4 December. Burrows were monitored at four sites on Lady Alice Island (Figure 4.1), each of which had a different vegetation type. The main canopy and subcanopy plants at each site were recorded (Appendix A). Adult attendance during incubation was monitored by using a 'fence' of twigs set up over the burrow entrance. Whenever a fence was displaced, the nesting chamber was checked to see if an incubating bird was present. When nests failed during the incubation stage, eggshell remains were collected and photographed, and nest material in the burrow was examined for evidence of the cause of failure. At the chick rearing stage burrows containing chicks were checked daily, and when burrows failed nest material was removed and examined for evidence of the cause of failure.

4.2.3 Obtaining evidence of kiore predation

A timelapse video camera with an infra-red light source was used at a nesting chamber which contained an incubating Little Shearwater. The roof of the nesting chamber was removed, and the camera was erected on top of a light-proof box, so that it pointed directly down into the chamber. The camera was run for a total of 157 hours over 11 nights. After one predation event was filmed, a depression was made in the nest material so that an egg could not easily be rolled out of the nesting chamber, and a punctured domestic hen egg was put in the nest in place of the depredated Little Shearwater egg.

A hen egg with a small hole made in it was placed in a cage with three captive kiore and left for several hours. Damage to the eggshell provided comparative material for identifying damage to Little Shearwater eggshells found in burrows where breeding failed during incubation.

Unless stated otherwise, results are given as the mean ± 1SD.

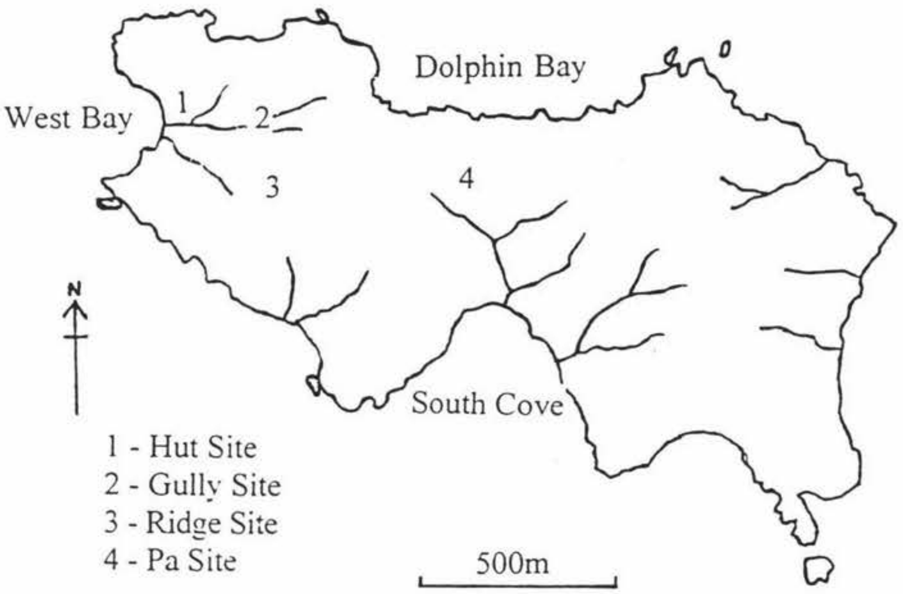


Figure 4.1: Location of study sites on Lady Alice Island.

4.3 **Results**

4.3.1 Little Shearwater breeding success

At the start of the breeding season, 29 burrows containing incubating Little Shearwaters were found. Eggs hatched at 13 (45%) of these nests. Of the 13 chicks monitored, 11 (85%) survived to fledging. Overall breeding success of Little Shearwaters during the 1994 breeding season was therefore 38%.

material so that an egg could not easily be rolled out of the nesting chamber, and a punctured domestic hen egg was put in the nest in place of the depredated Little Shearwater egg.

A hen egg with a small hole made in it was placed in a cage with three captive kiore and left for several hours. Damage to the eggshell provided comparative material for identifying damage to Little Shearwater eggshells found in burrows where breeding failed during incubation.

Unless stated otherwise, results are given as the mean ± 1SD.

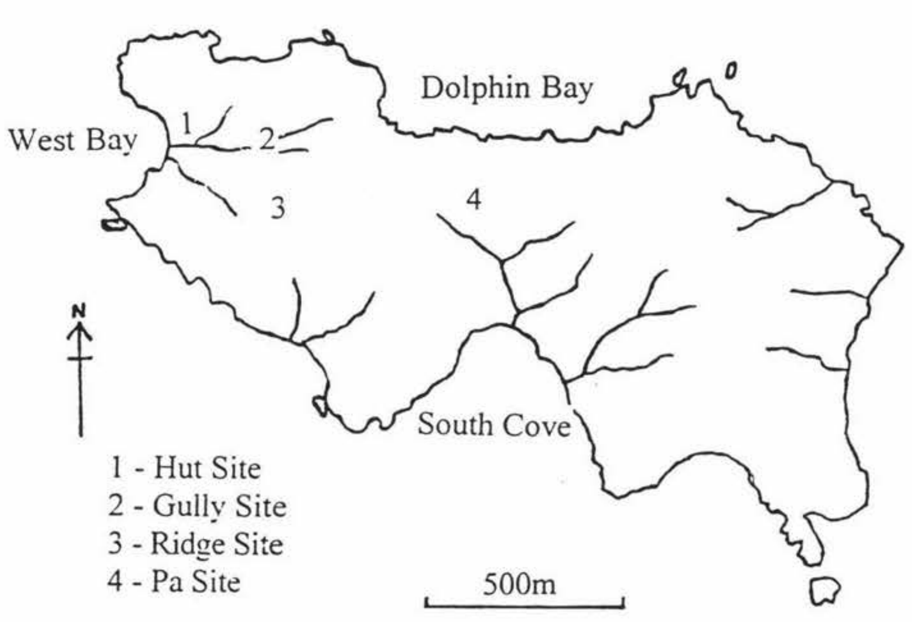


Figure 4.1: Location of study sites on Lady Alice Island.

4.3 **Results**

4.3.1 Little Shearwater breeding success

At the start of the breeding season, 29 burrows containing incubating Little Shearwaters were found. Eggs hatched at 13 (45%) of these nests. Of the 13 chicks monitored, 11 (85%) survived to fledging. Overall breeding success of Little Shearwaters during the 1994 breeding season was therefore 38%.

4.3.2 Causes of breeding failure

During incubation, predation by kiore was the suspected cause of failure for at least 12 (41%) of the 29 nests with eggs (Table 4.1). Eleven of these nests contained eggshells bearing signs of kiore damage. In the remaining nest the egg was removed overnight, and no trace of the egg was left in or around the burrow. Kiore droppings were also found in seven of the 12 burrows.

Two of the nests which failed during incubation showed no sign of the cause of failure. Both of these nests failed while I was absent from the study site. The eggshells recovered from the burrows were broken into many small pieces, presumably by adult Little Shearwaters returning to the burrow after breeding failure.

Little Shearwater adults were thought to have been the cause of failure for the remaining two nests which failed during incubation. At one of these nests a Little Shearwater was found incubating a broken egg, which had become stuck to its breast feathers. At the other nest a Little Shearwater was twice observed kicking the egg from the nesting chamber to the burrow entrance, after I had replaced the egg in the nest. The egg was later found broken in the burrow entrance.

Of the two chicks which did not survive to fledge, one was suspected to have been preyed on by kiore. This chick disappeared the night after it hatched, and had shown no signs of sickness prior to its disappearance. Fresh kiore droppings were found in the burrow, suggesting recent predation. The other chick disappeared while I was absent from the study site, and no sign of the cause of failure was found.

Overall, kiore predation was the major cause of breeding failure, accounting for at least 13 (72%) of the 18 nests which failed (check this against chpt 5 and abstract).

Table 4.1: Causes and timing of Little Shearwater breeding failure. ( ) = proportion of total nests monitored (n = 29).

	Cause of failure			
	Kiore	Unknown	Little Shearwater	Total
Incubation stage	12 (41%)	2 (7%)	2 (7%)	16 (55%)
Chick stage	1 (3%)	1 (3%)	0 (0%)	2 (7%)
Total	13 (45%)	3 (10%)	2 (7%)	18 (62%)

4.3.3. Timing of breeding failure

Nests were most likely to fail during incubation (Table 4.1), with 16 (89%) of the 18 unsuccessful nests failing at this stage. For nests where the date of failure during incubation was recorded, failure occurred at 42 ± 11.4 days after laying (range = 25 - 59, n = 9). Seven nests failed while I was absent from Lady Alice Island, and in these nests failure occurred at between 2 and 69 days after laying.

The date of failure for eggs was recorded for seven nests where I suspected predation by kiore. The mean number of days to failure after laying was 43 ± 9.2 (range = 29 - 56). The mean incubation period of the Little Shearwater on Lady Alice Island was 57 ± 1.1 days (n = 4), or approximately eight weeks (Chapter 2). Predation events were not distributed evenly throughout the incubation period. All predation events for which the date of failure was recorded occurred in the second half of the incubation period, with predation most likely during the sixth or seventh week after laying.

During the chick stage, the chick suspected as having been preyed on by kiore disappeared at one day old. The other chick disappeared between 11 and 39 days old.

4.3.4 Causes of breeding failure at each study site

The causes of breeding failure and overall breeding failure at each of the four study sites is shown in Table 4.2. There was a significant difference in the rate of breeding failure between sites ($\chi^2 = 14.816$, $df = 3$, $P < 0.001$), with no breeding failure at the Pa site, and 100% failure at the Ridge site. Breeding failure at the Hut and Gully sites was 50% and 33% respectively. Kiore predation was much higher at the Ridge site than at any of the other 3 sites ($\chi^2_c=9.9$, $p<0.005$), accounting for the failure of at least 75% of the nests with eggs.

Table 4.2: Comparison between sites of causes of breeding failure, and overall breeding failure of Little Shearwaters. ( ) = proportion of total eggs laid at that site.

		Cause of failure						
		Kiore		Unknown		Little Shearwater		Total
Site	eggs laid	egg stage	chick stage	egg stage	chick stage	egg stage	chick stage	Breeding failure
1 - Hut	8	2 (25%)	-	1 (13%)	1 (13%)	-	-	50%
2 - Gully	6	1 (7%)	-	-	-	1 (17%)	-	33%
3 - Ridge	12	9 (75%)	1 (8%)	1 (8%)	-	1 (8%)	-	100%
4 - Pa	3	-	-	-	-	-	-	0%

4.3.5 Breeding failure in relation to time eggs were left unattended

The proportion of days that eggs were left unattended by parents at each site is shown in Table 4.3. There was no significant difference in the length of time eggs were left unattended at each site (ANOVA $F_{[3,19]} = 0.36$, p=0.779).

Table 4.3. Percentage of days Little Shearwater eggs were left unattended at each study site.

Site	Eggs laid	% days unattended
1 - Hut	8	21
2 - Gully	6	12
3 - Ridge	12	12
4 - Pa	3	28

4.3.6. Evidence of kiore predation of Little Shearwater eggs

The video camera filmed a kiore removing an uncracked Little Shearwater egg from the nesting chamber at 0250hrs on 14 October 1994. This egg had been left unattended since 2025hrs on the previous night. The kiore tucked the egg under its chin (Figure 4.2), and removed it from the camera's field of view in nine seconds. No kiore visited this burrow again on the same night. The following morning the egg was recovered from the burrow where its contents had been eaten just out of view of the video camera. In the same burrow a kiore was filmed breaking open and eating a punctured hen egg in full view of the camera at 2035hrs on 14 October 1994. After this predation event, the nesting chamber was visited four times during the same night by a kiore for periods lasting between 7 seconds and *c*. 5 minutes. During these visits, the kiore searched through nest material in the nesting chamber.

4.3.7. Sign left by kiore on Little Shearwater and domestic hen eggs

The Little Shearwater egg which was filmed being removed from the nesting chamber by a kiore is shown in Plate 4.1(a). Damage to this egg was typical of sign left by other rat species, and included a large hole at the narrow end with a jagged edge where small pieces of eggshell (mean width = 0.5cm) had been broken off, and one distinctive set of incisor marks on the edge of the hole (Plate 4.2). The hen egg which was filmed being eaten by a kiore was broken into two large pieces, both of which had jagged edges. The hen egg placed in a cage with captive kiore is shown in Plate 4.1(b), and included a hole broken out of one side of the egg and jagged edges where small pieces of eggshell (mean width = 0.6cm) had been broken off. This

Figure 4.2: Kiore removing egg from the nesting chamber. Drawing taken from a video still.

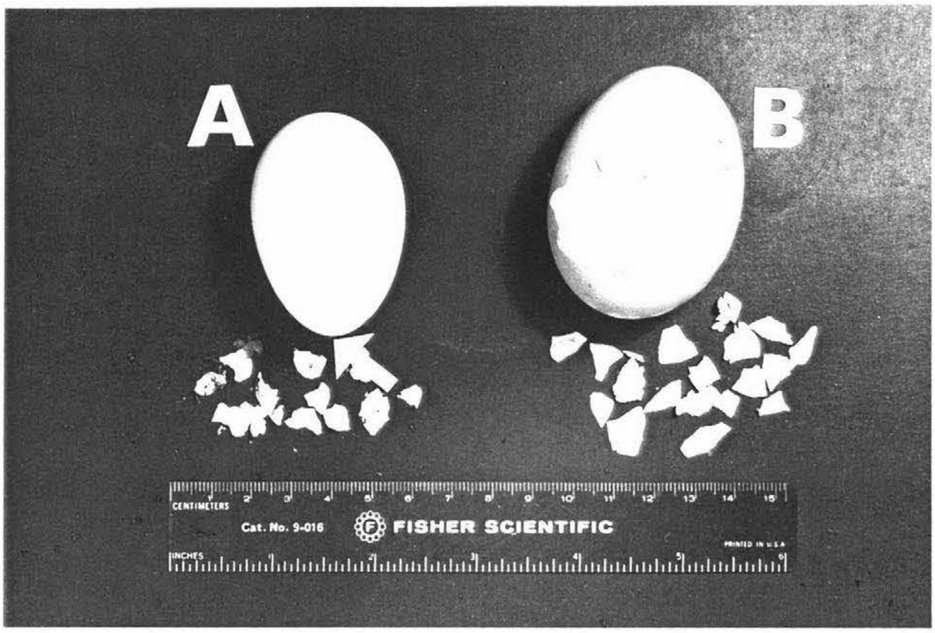


Plate 4.1: (a) Remains of the Little Shearwater egg which was filmed being removed from the nesting chamber by a kiore.
(b) Remains of the domestic hen egg placed in a cage with captive kiore.

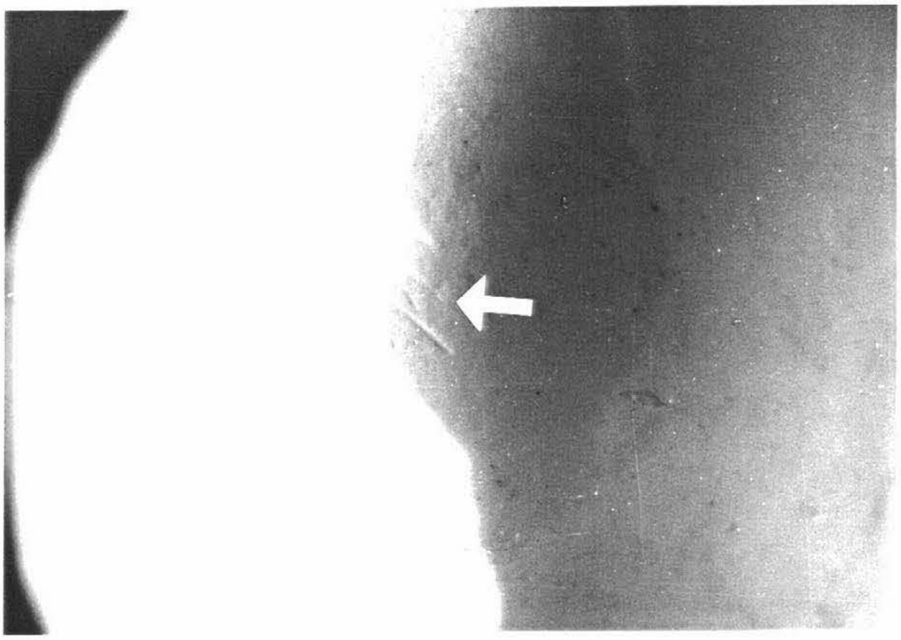


Plate 4.2: Kiore incisor marks on Little Shearwater egg in Plate 4.1 (a).

damage was similar to that on both the Little Shearwater egg and the hen egg which were filmed being interfered with by kiore. Neither of the hen eggs had incisor marks on them. Numerous pieces of eggshell from both the Little Shearwater and the hen egg were found spread throughout the nesting material, indicating that kiore "snuffle" or spread pieces of eggshell around inside the nest lining after preying on eggs. Kiore droppings were also found in the nest.

Sign similar to that described above was also found at the other nests which had incubation failure attribued to kiore predation. Complete removal of the egg was also characteristic of presumed predation; at one burrow the egg disappeared overnight and no eggshell remains were found in or around the burrow.

4.4 **Discussion**

The breeding success of the Little Shearwater population on Lady Alice Island was very low in 1994, with only 38% of nests producing chicks to fledging age. Predation by kiore of Little Shearwater eggs was the main cause of breeding failure (Table 4.1), and accounted for at least 12 (75%) of the 16 nests which failed during incubation.

Predation events occurred late in the incubation period, and may indicate that rats learn to exploit a new food source as the season progresses. Grant *et. al.* (1981) suggested that the removal and eating of petrel eggs is a learned behaviour by black rats (*R. rattus*), while Imber (1984) found an increasing rate of rat (*Rattus* spp.) predation of Gadfly Petrel (*Pterodroma* spp.) eggs through the incubation period, and also suggested rats learn to prey on eggs. However, other explanations for the increase in the rate of predation include alternative kiore food sources declining through the winter, or an increase in predation opportunities due to changes in behaviour of Little Shearwater adults. Whatever the reason, eggs were more likely to be preyed on later in incubation.

Kiore predation was much higher at the Ridge site than at any of the other three sites (Table 4.2). The composition and density of the main canopy species differed between sites (Appendix A). At the ridge site, the predominant canopy species was kanuka (*Kunzea ericoides*), and this site was drier than the other three due to its north-facing aspect (Figure 4.1). The high rate of predation at this site may have been influenced by the vegetation, and the resulting composition and abundance of alternative food sources for kiore. If there was less plant material and invertebrate prey available for kiore at the Ridge site than at the other three sites during the Little Shearwater incubation period, there may have been more pressure on kiore to exploit an alternative food source such as seabird eggs. However, as neither kiore density or alternative food abundance was measured at any of the sites, I could not determine what factors were influencing the high predation rate at the Ridge site. Alternatively, the high predation rate may have been due to a group of kiore learning to exploit this food supply. Woodward (in Grant *et. al.* 1981) suggested that a group of kiore learned to attack nesting albatrosses on Kure Atoll, Hawaii. Further research is required to determine the factors which influence the rate of predation by kiore on seabird eggs and chicks.

Behavioural and size differences between bird species influence their susceptability to rat predation (Moors *et. al.* 1992). Several aspects of the behaviour of the Little Shearwater during the breeding season may increase its vulnerability to predation by kiore. Firstly, Little Shearwater eggs are frequently left unattended during the incubation period. Temporary absence during incubation is common behaviour in many procellariiform birds (Boersma & Wheelwright 1979, Chaurand & Weimerskirch 1994), in which the embryos can survive intermittent chilling. Little Shearwater eggs were found unattended in at least 77% of the burrows on Lady Alice Island for periods averaging 1.9 ± 1.5 days (n = 26) (Chapter 2). Such behaviour by incubating birds may increase the vulnerability of eggs to rat predation (Imber 1984). It would appear, however, that the degree of predation is not directly related to the degree of temporary unattendance, for although the predation rate varied greatly between sites (Table 4.2), the rate at which eggs were left unattended did not (Table 4.3). Secondly, chicks start pipping up to eight days before hatching (*pers. obs.*), and adults often leave eggs unattended for a night at this stage, presumably to feed before the chick hatches. A combination of the eggshell being cracked by the emerging chick and a high rate of non-attendance makes Little Shearwater eggs especially vulnerable just before hatching.

The video footage of a kiore removing a Little Shearwater egg from the burrow provides the first direct evidence of kiore preying on seabird eggs in New Zealand (Figure 4.2). Recovery next morning of this egg showing signs of rat damage left no doubt that kiore prey on the eggs of the Little Shearwater.

It is very important to identify the sign left by different mammalian predators, because this is usually the only way that a predator can be identified after a predation event (Moors 1978). The sign left by kiore after preying on Little Shearwater eggs (Plates 4.1 and 4.2), including clean removal of eggs, is very similar to sign left in birds' nests by other rat species (Moors 1975, Moors 1978, Major 1991).

After establishing that an introduced mammal is preying on a bird species, it is important to determine whether this induces population decline (Moors 1983, Moors *et al.* 1992), so that appropriate management decisions can be made. The long-term impact of kiore predation on seabirds and other native species is a contentious issue.

Atkinson and Moller (1990) implicated kiore in the extinction of mainland petrel species such as Cook's Petrels. Craig (1986), however, suggested that the evidence of kiore impacts on endemic biota was equivocal and circumstantial, with no direct evidence that kiore reduce seabird numbers. The impact of kiore on the Little Shearwater population on Lady Alice Island was very high during the 1994 breeding season, with 62% of all nests failing, and predation by kiore suspected to be the cause of failure for at least 75% of the nests which failed. In order for this rate of predation to cause a decline in the Little Shearwater population over time, losses to the population due to kiore predation would have to cause annual mortality to exceed annual recruitment (Moors 1983). At this stage the impact of kiore on seabird populations is unknown, although it would be prudent management to minimise the impact of a predator responsible for a such a high rate of nesting failure. Even small rates of loss from predation may be enough to cause insufficient recruitment in a population (Moors 1983).

Kiore were eradicated from Lady Alice Island in October 1994, so there is now the opportunity to monitor the breeding success of the Little Shearwater in the absence of kiore. Breeding success of the Little Shearwater on Lady Alice Island was also monitored in 1993 (50% breeding success, n = 20; R. J. Pierce, *unpubl.*), providing records of productivity in the presence of kiore for two successive years. Continued monitoring of the population will determine whether annual productivity is higher after kiore have been eradicated. The best indication of the impact of kiore predation on the Little Shearwater will be whether the recruitment rate, and therefore population density, increases after the eradication. The age at which Little Shearwaters first breed is unknown. The closely related Manx Shearwater *P. puffinus* breeds at about five years of age (Harris 1966) and the Little Shearwater may have a similar breeding age. It will, therefore, be necessary to continue studies beyond five years hence to measure recruitment and thus assess the extended impact of kiore on the Little Shearwater population. In the mean time, if annual productivity increases, this would indicate a beneficial effect of kiore eradication.

4.5 **References**

Atkinson, I.A.E.; Moller, H. 1990. Kiore, *Rattus exulans* (Peale, 1848). Pages 175-192 *in* King, C.M. (ed.) The Handbook of New Zealand Mammals. Auckland: Oxford University Press.

Bell, B.D. 1986. The conservation status of New Zealand wildlife. New Zealand Wildlife Service Occasional Publication No. 12; Department of Internal Affairs, Wellington.

Boersma, P.D.; Wheelwright, N.T. 1979. Egg neglect in the Procellariiformes: reproductive adaptations in the Fork-tailed Storm-petrel. Condor 81: 157-165.

Cameron, E.K. 1984. Vascular plants of the three largest Chickens (Marotere) Islands: Lady Alice, Whatupuke, Coppermine: North-east New Zealand. Tane 30: 53-75.

Chaurand, T.; Weimerskirch, H. 1994. Incubation routine, body mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. Ibis 136: 285-290.

Craig, J.L. 1986. The effects of kiore on other fauna. Pages 75-83 *in* Wright, A.E.; Beever, R.E. (eds.) The offshore islands of northern New Zealand. Wellington: New Zealand Department of Lands and Survey Information Series.

Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20: 115-120.

Fleet, R.R. 1972. Nesting success of the Red-tailed Tropicbird on Kure Atoll. Auk 89: 651-659.

Glauert, L. 1946. The Little Shearwater's Year. Emu 46: 187-192.

Grant, G.S.; Pettit, T.W.; Whittow, E.C. 1981. Rat predation on Bonin Petrel eggs on Midway Atoll. Journal of Field Ornithology 52: 336-338.

Harris, M.P. 1966. Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. Bird Study 13: 84-95.

Imber, M. 1978. The effects of rats on the breeding success of petrels. Pages 67-72 *in* Dingwall, P.R.; Atkinson, I.A.E.; Hay, C. (eds.) The ecology and control of rodents in New Zealand nature reserves. Wellington: Department of Lands and Survey Information Series.

Imber, M.J. 1984. Exploitation by rats of eggs neglected by Gadfly Petrels. Cormorant 12: 82-93.

Jane, G.; Beever, R.E. 1965. A list of the vascular plants of Motu Muka (Hen and Chickens Group). Tane 11: 87-91.

Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. Auk 84: 426-430.

Major, R.E. 1991. Identification of nest predators by photography, dummy eggs, and adhesive tape. Auk 108: 190-195.

Moors, P.J. 1975. Introduced predators and the South Island Robin. Wildlife - a review 6: 26-31.

Moors, P.J. 1978. Methods for studying predators and their effects on forest birds. Pages 47-56 *in* Dingwall, P.R.; Atkinson, I.A.E.; Hay, C. (eds.) The ecology and control of rodents in New Zealand nature reserves. Wellington: Department of Lands and Surveys Information Series 4.

Moors, P.J. 1983. Predation by mustelids and rodents on the eggs and chicks of native and introduced birds in Kowhai Bush, New Zealand. Ibis 125: 137-154.

Moors, P.J.; Atkinson, I.A.E. 1984. Predation on seabirds by introduced animals, and factors affecting its severity. I.C.P.B. Technical Publication No 2: 667-689.

Moors, P.J.; Atkinson, I.A.E.; Sherley, G.H. 1992. Reducing the rat threat to island birds. Bird Conservation International 2: 93-114.

Percy, C.A. 1955. A primary study of the vegetation of Marotiri Island. Tane 7: 3-6.

Thoresen, A.C. 1967. Ecological observations on Stanley and Green Islands, Mercury Group. Notornis 14: 182-200.

Turbott, E.G. 1990. Checklist of the Birds of New Zealand. Random Century In association with the Ornithological Society of New Zealand:

Warham, J. 1955. Observations on the Little Shearwater on the nest. Western Australian Naturalist 5: 31-39.

Warham, J. 1958. Photographic studies of some less familiar birds. XCII Little shearwater. British Birds 51: 393-397.

Wirtz, W.O. 1972. Population ecology of the Polynesian Rat, *Rattus exulans*, on Kure Atoll, Hawaii. Pacific Science 26: 433-464.

Chapter Five: Summary and Conclusions

This is the first study to investigate the breeding ecology of the Little Shearwater in detail, and provides the first published record of the breeding ecology of the North Island sub-species of Little Shearwater.

Several aspects of the breeding ecology of the Little Shearwater indicate that environmental conditions during the breeding season have not resulted in selection for behavioural or physiological characteristics observed in other Procellariiformes.

Firstly, the Little Shearwaters in this study exhibited a high degree of intra-population asynchrony in laying relative to other procellariiform species. Synchronous laying in the Procellariiformes is generally thought to be influenced by a variation in food availability during the breeding season. If food availability reaches a peak early in the season, laying synchrony may result from females utilising this to aquire food for egg formation. Alternatively, laying synchrony may be influenced by an increase in food supply during the chick rearing period, so that chicks are being reared during a period of optimum food availability. The extent of asynchrony in laying in the Little Shearwater suggests that either food availability does not fluctuate significantly during the breeding season, or that any variation in food supply is not large enough to influence the timing of laying. An alternative explanation for the asynchrony in laying may be that there is an optimum time to lay for the Little Shearwater, but a reduction or some other change in the food supply has meant that females can not all lay at the same time. Determining the breeding success of individuals in relation to their timing of laying would indicate whether there is an optimum time for laying in this species.

The second factor which suggests that environmental conditions during the breeding season do not have a major effect on the Little Shearwater is the lack of correlation between the egg volume index and the timing of laying. Several studies have shown that the egg size of pelagic seabirds decreases during the laying period. If food supply declines throughout the season, this physiological strategy may result in late breeding females minimising the delay in laying. However, in order to determine whether a decrease in egg size leads to eggs being laid earlier, one would need to determine whether the length of the period between copulation and laying was correlated with egg size.

Thirdly, the behaviour of Little Shearwater adults during the chick rearing period indicates that if food availability at this stage is unpredictable, it does not affect the food provisioning ability of adults. The role of large fat reserves in procellariiform chicks is uncertain, although it has been suggested that this characteristic provides insurance against a patchy and unpredictable food supply (Lack 1968). I determined the frequency of food delivery by adults by either monitoring adult visitation or weighing chicks, and found that chicks were fed, on average, on 94% of nights (n = 241). Furthermore, there was no obvious difference in the proportion of nights chicks were fed in relation to their age. These results are not compatible with the theory that fat reserves are insurance against a stochastic food supply, because chicks were fed regularly. However, the food provisioning behaviour of adults needs to be studied over several years to determine whether regular feeding of chicks is typical for this population. Food availability may fluctuate between years, and further research would determine whether there is a temporal variation in food provisioning for this species.

This study presents the first known record of procellariiform parents coordinating food provisioning visits to the chick. Previous studies have found that adults feed the chick independently of one another (Ricklefs *et. al.* 1985, Chaurand & Weimerskirch 1994, Weimerskirch *et. al.* 1994). Ricklefs & Schew (Ricklefs & Schew 1994) suggested that fat reserves in Procellariiformes provide insurance against stochastic variation in the food provisioning ability of adults, rather than an unpredictable food supply. They also suggested that independent foraging by adults increases the variance in food delivery to chicks due to variability in the in the length of the feeding interval. As Little Shearwater pairs coordinated feeding shifts, there was, however, less possibility for chicks to be left unfed for long periods than for those Procellariiformes which forage independently. My results are in contrast to those of other studies of procellariiform foraging behaviour, and cast doubt on the theory that fat deposits provide insurance against adult foraging ability, at least for the Little Shearwater. I suggest that coordination of feeding shifts may provide information to each adult about the nutritional status of the chick, thus providing an opportunity for adults tò regulate food delivery. This is supported in part by the proportion of body mass lost by Little Shearwaters between obtaining maximum mass and fledging, which is less than that of other Procellariidae (Warham 1990). It would appear that Little Shearwater chicks do not accumulate as much fat relative to their body size as other members of this family. Further research is needed to determine whether Little Shearwater adults are regulating food delivery to chicks.

Circumstantial evidence of extra-pair copulations has not previously been noted in this species. Because Little Shearwaters lay eggs over an extended period (62 days), the mating period must be a similar length or longer. For monogamous birds, males can reduce the risk of mates being fertilised by another male by mate guarding and frequent copulations (Birkhead 1987). For the Little Shearwater, opportunities for extra-pair copulations may arise if pairs do not synchronise their return to the breeding ground to mate. For males, the advantages of extra-pair copulations include an increase in both offspring production and breeding lifespan, while females may use this strategy to insure against infertile mates (Austin *et. al.* 1993). In order to determine unequivocally that extra-pair fertilisations take place in the Little Shearwater, evidence in the form of DNA fingerprinting is required.

This study provides the first direct evidence of predation by kiore (*Rattus exulans*) of the eggs of the Little Shearwater. Kiore predation had a high impact on the breeding success of the Little Shearwater population on Lady Alice Island in 1994. Egg predation occurred late in incubation, and appeared to be influenced by vegetation type. However, further research is required to determine whether the rate of kiore predation on the eggs of small seabirds differs between sites with different vegetation. Little Shearwaters frequently leave eggs unattended, which may increase the vulnerability of eggs to predation. The rate at which adults leave eggs unattended should be a consideration when predicting the vulnerability of a seabird species to predation by kiore and other *Rattus* spp. The rate of kiore predation was likely to have been high enough to result in insufficient recruitment to maintain the population. In order to determine the long-term impact of kiore predation, a population should be monitored for several years to determine any temporal variation in the rate of predation. Kiore have now been eradicated from the study site, so we can not test whether the degree of predation recorded in this study was typical. By continuing to monitor the Little Shearwater population on Lady Alice Island, we will see whether the population increases in the post-eradication period. If it does, this would strongly suggest that eradication of kiore results in an increased recruitment rate, and a subsequent increase in the shearwater population.

Pycroft's Petrels (*Pterodroma pycrofti*) also breed on Lady Alice Island, and are listed as endangered (Bell 1986). This species breeds in the summer, and the timing of return to the breeding ground to lay coincides with the end of the chick rearing period of the Little Shearwater. The two species sometimes utilise the same burrows for breeding (*pers. ob.*). At present, there appears to be an excess of seabird burrows on Lady Alice Island, possibly following a decline in seabird numbers from kiore predation. If seabird numbers now increase, this could result in competition for burrows between Pycroft's Petrels and Little Shearwaters. The interaction between these two seabird species should be monitored, in order to determine whether an increase in the population size of one species could result in inter-specific competition for nest sites.

REFERENCES

Austin, J.J.; Carter, R.E.; Parkin, D.T. 1993. Genetic evidence for extra-pair fertilisations in socially monogamous Short-tailed Shearwaters, *Puffinus tenuirostris* (Procellariiformes: Procellariidae), using DNA fingerprinting. Australian Journal of Zoology 41: 1-11.

Bell, B.D. 1986. The conservation status of New Zealand wildlife. New Zealand Wildlife Service Occasional Publication No. 12; Department of Internal Affairs, Wellington.

Birkhead, T.R. 1987. Sperm competition in birds. Trends in Ecology and Evolution 2: 268-272.

Chaurand, T.; Weimerskirch, H. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea* : a previosly undescribed strategy of food provisioning in a pelagic seabird. Journal of Animal Ecology 63: 275-282.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd.: London.

Ricklefs, R.E.; Day, C.H.; Huntington, C.E.; Williams, J.B. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. Journal of Animal Ecology 54: 883-898.

Ricklefs, R.E.; Schew, W.A. 1994. Foraging stochasticity and lipid accumulation by nestling petrels. Functional Ecology 8: 159-170.

Warham, J. 1990. The petrels, their ecology and breeding systems. Academic Press: London.

Weimerskirch, H.; Chastel, O.; Ackermann, L.; Chaurand, T.; Cuenot-Chaillet, F.; Hindermeyer, X.; Judas, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. Animal Behaviour 47: 472-476.

APPENDIX A: Canopy and sub-canopy plant species at each of the four study sites

Site 1 - Hut

Canopy

Carmichaelia aligera	North Island broom
Coprosma spp.	-
Cordyline australis	cabbage tree
Dysoxylum spectabile	kohekohe
Geniostoma rupestre	hangehange
Leptospermum ericoides	kanuka
Melicytus ramiflorus	whiteywood
Metrosideros excelsa	pohutukawa
Pseudopanax arboreus	five-finger
P. lessonii	houpara
Cyathea spp.	ponga

Sub-canopy

Brachyglottis repanda	rangiora
Clematis spp.	clematis
Coprosma spp.	-
Dysoxylum spectabile	kohekohe
Geniostoma rupestre	hangehange
Hebe spp.	-
Macropiper excelsum	kawakawa
Myrsine australis	mapou
Olearia furfuracea	akepiro
Phormium tenax	flax
Sophora microphylla	kowhai

Site 2 - Gully

Canopy

Corynocarpus laevigatus	karaka
Dysoxylum spectabile	kohekohe
Leptospermum ericoides	kanuka
Melicytus ramiflorus	whiteywood
Metrosideros excelsa	pohutukawa
Nestegis apetala	coastal maire
Sophora microphylla	kowhai
Vitex lucens	puriri

Sub-canopy

Brachyglottis repanda	rangiora
Hoheria populnea	lacebark

Macropiper excelsum	kawakawa
Myrsine australis	mapou
Pisonia brunoniana	parapara
Pseudopanax arboreus	five-finger
Rhabdothamnus solandri	waiuatua

Site 3 - Ridge

Canopy

Carmichaelia aligera	North Island broom
Dysoxylum spectabile	kohekohe
Leptospermum ericoides	kanuka
Melicytus ramiflorus	whiteywood
Pittosporum umbellatum	haekaro
Pseudopanax arboreus	five-finger
Sophora microphylla	kowhai

Sub-canopy

Brachyglottis repanda	rangiora
Coprosma spp.	-
Geniostoma rupestre	hangehange
Hebe spp.	-
Hoheria populnea	lacebark
Macropiper excelsum	kawakawa
Myrsine australis	mapou
Olearia spp.	-
Phormium tenax	flax
Pseudopanax arboreus	five-finger

Site 4 - Pa

Canopy

Beilschmiedia tarairi	taraire
Dysoxylum spectabile	kohekohe
Knightia excelsa	rewarewa
Leptospermum ericoides	kanuka
Metrosideros excelsa	pohutukawa
Nestegis apetala	coastal maire
Vitex lucens	puriri

Sub-canopy

Brachyglottis repanda	rangiora
Carmichaelia aligera	North Island broom
Coprosma spp.	-
Geniostoma rupestre	hangehange

Hedycarya arborea	pigeonwood
Hoheria populnea	lacebark
Macropiper excelsum	kawakawa
Melicytus ramiflorus	mahoe
Myrsine australis	mapou
Olearia spp.	-
Pittosporum umbellatum	haekaro
Pseudopanax arboreus	five-finger