

Effectiveness of parental provisioning under variable oceanographic conditions along the Western Australian coast in two shearwater species: the Little Shearwater *Puffinus assimilis tunneyi* and the Wedge-tailed Shearwater *Puffinus pacificus*.

A thesis presented for the degree of Doctor of Philosophy,  
School of Biological Sciences and Biotechnology,  
Murdoch University, Western Australia.

Indre Kirsten Asmussen BSc (Hons)  
2006

## **Declaration**

I declare that this thesis is my own account of my research  
and contains as its main content work,  
which has not previously been submitted for a degree  
at any tertiary education institution.

.....

Indre Kirsten Asmussen

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## Abstract

Parental provisioning was investigated in two congeneric shearwater species, the winter breeding Little Shearwater *Puffinus assimilis tunneyi* and summer breeding Wedge-tailed Shearwater *Puffinus pacificus*. The Western Australian coast is characterised by climatic and oceanographic instability largely linked to the variable flow rate of the Leeuwin Current generated by differences in global climatic conditions. Ongoing long-term studies at the Western Australian coast have indicated that this climate driven phenomenon affects seabird reproductive participation and success. Such an ongoing, parallel study of Wedge-tailed Shearwater reproduction effectively provided this thesis with a background index of oceanographic conditions, or a context in which to view and interpret the ability of adults to provide parental care to the dependent nestling. Such an index of oceanographic conditions is generally lacking in studies of seabird provisioning. Fortuitously, this study was conducted in what appeared to be a favourable year (2000), a transition year (2001) and a less favourable year (2002) for seabird reproduction off the Western Australian coast. Consequently, it was possible to comment on the effectiveness of parental provisioning during different oceanographic conditions.

In this thesis, parental provisioning encompassed the delivery of a range of resources to the dependent nestling, including a burrow, heat during incubation, protection from predators, brooding after hatching, and the delivery of food to sustain growth and development. The main focus of the study was the nestling feeding stage, although other more sensitive and less flexible phases were investigated in the Little Shearwater. Most research focused on the winter breeding Little Shearwater, as the

species least studied. Adult Little Shearwaters were present at the nest throughout the night during the nestling feeding period, which presented the opportunity to examine provisioning from an adult perspective. Adult responses are discussed in the context of this index of oceanographic condition, in terms of regional food resources levels, and also more localised weather patterns which facilitate shearwater locomotion. A potential two-tier adult state-dependent mechanism of parental resource allocation is presented, which would allow a mobile K-strategist, foraging within an acceptable distance from the breeding colony, to persist in this relatively unstable and unpredictable environment.

This research suggests that parents' adjusted parental provisioning in order to minimise risks to the functional adult, which had attained its reproductive potential at the expense of the nestling that may or may not attain reproductive status. The weights of adult encountered at the colony did not differ significantly between different phases of the breeding season (pre-laying, incubation and nestling feeding) or between years. It appeared as if the weights of adults engaged in parental provision fluctuated within an acceptable "working" range whilst present at the colony, which makes it difficult to define average adult weights. The theory of threshold adult body condition suggests that only adults above a sufficient body condition are allocating resources towards reproduction, and therefore present at the breeding colony. Whilst, adults below a threshold are expected to be absent from the colony and therefore not willing to allocate resources to support the dependent nestling.

In the two-tier adult state dependent allocation of parental care, firstly the body condition of the adult will determine if it is present at the colony, hence providing

care for the offspring. Secondly if the adult is able to maintain adult body condition provisioning can be reactive to the needs (or body condition) of the nestling.

Evidently, such a system of parental provisioning predominantly based on the ability to maintain adult body condition will be affected by differences in oceanographic and climatic conditions, which affect the ability of adults to maintain or replenish body condition within an acceptable time and distance away from the colony. The level and continuity of parental care provided by the pair will be discussed, especially how deviations from an optimal provisioning schedule may affect nestling growth, survival and viability.

Ongoing, long term research of summer breeding Wedge-tailed Shearwaters along the Western Australian coast suggests that reproduction is adversely affected by prevailing negative southern oscillation indices and associated declines in the flow rate of the warm, low density Leeuwin Current. Despite breeding in the austral winter when the maximal flow rates of the Leeuwin Current are expected, Little Shearwater reproduction was also affected in a manner similar to that documented for tropical seabirds breeding in summer. Furthermore, decreases in productivity registered by local fisheries suggested that observed declines in seabird reproduction may be linked to an overall crash in productivity experienced along the Western Australian coast during years of weak Leeuwin Current flow. Such years are associated with more uniform and cold offshore water temperatures. Consequently, a regional lack of oceanographic resources, within an acceptable distance of the breeding site, are likely to adversely affect the ability of adults to replenish body condition, however other factors such as prevailing weather are also likely to affect energy expenditure during

travel and foraging. Both factors would affect the ability of adults' to maintain body conditions.

In a favourable year, Little Shearwaters were able to meet nestling needs and the amount of food delivered matched the pattern of weight gain typical for Procellariiform young. Conversely, in a less favourable year, Little Shearwaters delivered food to young less often and the amount delivered was erratic, as the percentage of nestlings fed was consistently lower and temporal delivery was more irregular in the less favourable year. Nonetheless, food delivery also changed with nestling age, following a pattern similar to a favourable year, but at a lower rate. Future research should focus on the level of obesity attained by cohorts under different conditions and possibly the quality of feathers produced by nestlings. Feather quality and the state of obesity attained may affect the post-fledging buffer and ultimately affect fledging survival.

Supplementary feeding suggested that adult Wedge-tailed Shearwaters adjusted feeding in response to proximal needs of nestlings, as supplementary fed nestlings were fed less than non-supplementary fed nestling. Furthermore, in both species adults changed provisioning to meet the changing needs of nestlings throughout ontogeny however the adult's ability to respond to changing needs may be dependent upon the body condition of the adult and therefore ultimately dictated by resource availability. These results are in accord with other studies in which adults have altered provisioning in response to changing nestling needs. Whilst in other studies adults displayed an inability to react to nestling needs, which may have been linked to



the difficulty faced by adult to maintain their own body condition during a less favourable year.

The tentative mechanism of parental provisioning may help to explain the often contradictory outcomes recorded in studies of parental provisioning conducted in the absence of an indicator of resources availability and context in which to interpret adult response. Since, adults adjusted provisioning to firstly match their ability to maintain their own body condition in response to oceanographic conditions and secondly if able to met their own needs, in accordance with nestling needs.

Therefore, parental provisioning is a flexible, state-dependent behaviour ultimately limited by oceanographic conditions.

Once nestlings have hatched and passed a critical weight, they are more likely to survive and parental provisioning has the potential to become a highly flexible behaviour as the offspring can absorb periods of reduced parental provisioning. This relatively “forgiving” nestling phase is often targeted by studies of parental provisioning. Here, an optimal provisioning schedule may be orchestrated under favourable conditions however deviations may be absorbed without terminating the investment in reproduction.

Although breeding at different times of the year, both species fed their nestling to a stage of obesity. This occurred, despite feeding nestlings near daily, which should have allowed adults to obtain regular feedback about the body condition of the nestling. Obesity may reflect the relatively unpredictable availability of resources along the Western Australian coast. However, adults may aim to increase the

potential fitness of the nestling when adult body condition allows, through the provision of a post fledging buffer in terms of stored energy and high quality, structurally sound plumage.

At the Western Australian coast, Little Shearwaters used a bimodal strategy to care for nestlings during incubation and feeding. Adults lost weight during periods of intensive provisioning, namely incubation and nestling feeding, but if too much weight was lost, provisioning was withheld and adults departed for a longer absence. Whilst absent from the colony for a prolonged period of time adults gained weight, both during the incubation and nestling feeding period. Return of birds from long absences appeared to be related to the predictable passage of weather systems.

In Little Shearwater, during incubation the efforts of both parents were highly coordinated in a favourable year, since egg neglect was low, presumably as a consequence of predation pressure. Weather appeared to assist in the arrival of the relieving adult during incubation. Similarly during the transition to nestling feeding, the nocturnal activity at the breeding site indicated that the return of adults from long absences was associated with predictable changes in wind direction, related to the inevitable passage of weather systems, rather than wind strength, which is directly proportional to pressure differences between adjacent weather systems.

In a favourable year, during nestling feeding the co-ordination of change overs between individuals within a pair also appeared to be high. Consequently, patterns of provisioning may be entrained throughout the duration of the breeding season, including incubation and nestling feeding, by an underlying pattern generated by the

predictable passage of weather systems. Adults able to meet their own needs in a time frame dictated by the movement of weather system may minimise travel costs, whilst returning in time to allow the partner to depart to meet its needs. Both partners are required for the co-ordination of parental care to produce an optimal provisioning schedule. Consequently, activities are expected to be structured to protect not only the body condition of the self, but also of the partner in a species where biparental care is generally required to successfully raise an offspring.

During nestling feeding, in a favourable year the co-ordinated bimodal strategy achieved near daily delivery of food, whilst in a less favourable year deviations from this pattern occurred, as adults spent more time at sea. The average duration of long absences, used to replenish body condition, appeared to increase during less favourable years. Further research should focus on variations in temporal absences and adult weights under different conditions that affect the ability of adults to replenish their body conditions. Furthermore, not all pairs were able to achieve daily food delivery during each year, and during a less favourable year a larger proportion of the breeding population appeared to be unable to deliver continuous parental care. Consequently, a larger proportion of nestlings remained unfed. The disruption in the input system, or deviations from a potentially optimal provisioning schedule, resulted in differences in growth rates between years. Costs incurred by adults during less favourable conditions appeared to be passed on to the nestling, whilst the risks to the functional adult that had reached reproductive potential were minimised.

Wedge-tailed Shearwaters, breeding during the austral summer in a favourable year, were able to meet nestling needs. Here, food was delivered at a pattern that matched

weight gain, where total overnight food delivered changed with nestling age, as in the Little Shearwaters. Wedge-tailed Shearwaters did not deliver food as regularly as Little Shearwaters. The colony of Wedge-tailed Shearwaters appeared to experience periods of reduced provisioning, during low wind conditions associated with dissipating tropical lows. During such conditions, Wedge-tailed Shearwater adults were often seen rafting at sea away from the breeding site suggesting it was energy expensive to fly. Such periods of poor provisioning associated with low wind speeds were recorded at different latitudes along the Western Australian coast and in different years. Dissipating tropical lows which generate low wind conditions are a seasonal occurrence however the frequency, persistence and intensity of such tropical lows appeared to fluctuate with offshore sea surface temperatures, frequency of tropical cyclones to the north and ultimately prevailing large scale climatic conditions that affect sea surface temperatures. Consequently, prevailing short term weather conditions which are affected by large scale climatic events, including climate change, have the potential to influence Wedge-tailed Shearwater reproduction.

Wedge-tailed Shearwater nestlings supplementarily fed during a dissipating tropical low were visited and fed less than unfed nestlings of lower body condition. This implies that adults adjusted provisioning in accordance with nestling body condition. However, nestlings that had not been supplementarily fed were visited less often once conditions improved, suggesting that parents were unable to sustain food delivery. Parents of supplementarily fed nestlings, which had reduced provisioning during the adverse conditions, were able to feed their nestlings at a higher rate once conditions recovered than parents with non-supplementary fed nestlings. Thus, parents appeared to adjust provisioning in relation to nestling body condition however the ability of

adults to maintain high levels of parental care appears to be limited, possibly by parental body condition. Similarly, adults reacted to the changing needs of a nestling throughout ontogeny in a favourable year, whilst during an adverse year deviation from a more optimal pattern of provisioning was evident.

Meal sizes delivered by different species are often compared. However, food delivery appears to be adjusted with nestling age and differences in oceanographic conditions. Consequently, an optimal amount of food matching the developmental needs of the nestling may be met during optimal conditions using an optimal pattern of provisioning, whilst deviations from this may give an index of parental inability to cope with long or short-term deterioration in oceanic conditions, which ultimately affect their ability to meet adult needs. Furthermore, meal sizes are often determined during frequent weighing research of short duration, which is easily affected by proximal conditions that could affect the ability of adults to travel and would reflect the developmental stage of the nestling. Therefore, for meal sizes quoted it is not know if adults were able to engage in an optimal provisioning schedule or if deviations occur to compensate for below optimal conditions.

Comparison of meal size by weight alone may not be feasible, even throughout a season within a species, as a seasonal shift in diet was recorded for Wedge-tailed Shearwaters during the breeding season using stable isotope. The different diets of different species often living in different geographic locations and the ability of some species to produce stomach oil, further confounds the ability to compare meal sizes by weight alone. It appears difficult to define a meal size characteristic for a species and make direct comparisons based on weight alone a practice widespread in seabird

research. At best an optimal meal size for a given developmental stage may be used in conjunction with calorific values to calculate an optimal energy input for a specific age to compare between species.

The seasonal difference in diet recorded during the Wedge-tailed Shearwater breeding season revealed a shift from a higher to a lower trophic level. This is consistent with females engaging in a pre-laying exodus where preferred resources may be targeted, whilst during nestling feeding foraging constraints are introduced as foraging occurs around a central location. A broader range of prey may be targeted within an acceptable distance from the breeding colony, including scavenging behind Western Rock Lobster fishing vessels which provide a predictable source of food – or discarded often imported bait.

The application of stable isotope analysis provided promising insights into shearwater foraging behaviour otherwise difficult to elucidate. Different resources were targeted by the two species during egg membrane formation. Wedge-tailed Shearwaters generally appeared to forage at a higher trophic level than Little Shearwaters, although outliers suggest that Little Shearwaters also have the potential to target higher trophic levels. Differences in diet during egg formation were evident between different colonies of Wedge-tailed Shearwaters breeding at different locations. Consequently, stable isotope analysis may be used to track changes in diet between favourable and less favourable years, where increased foraging constraints are expected to emerge. Stable isotope analysis is a promising technique and interpretation of data will increase with further understanding of ecosystem dynamics and the development of a reference library.

Direct observation at sea suggested that Little Shearwaters forage in deep, offshore in areas most likely influenced by the Leeuwin Current. They were not observed to forage in the cooler, inshore waters fed by a northwards flowing counter current, on the continental shelf between the Houtman Abrolhos Islands and the mainland.

Maximum depth gauges revealed a maximal dive depth of approximately 34 m. The maximal dive depths recorded appeared to increase with time spent at sea, as indicated by birds engaged in short absences (near daily returns) from the colony and long absences (approximately weekly returns) when they were replenishing body condition. Long absences were recorded after an incubation shift or a period of daily nestling feeding.

To summarise, a tentative mechanism of adult state-dependent allocation of parental provisioning in which pelagic seabirds persist in environments of fluctuating resource levels was proposed. This may be based upon the ability of adults to operate above a threshold body condition, which is ultimately dictated by resource availability and proximal conditions which affect the ability of adults to maintain their own body condition. Once adults struggle to maintain their body condition, a disruption in the co-ordination of the parental care orchestrated between the members of a pair can arise, as adults spend more time away from the colony replenishing their body condition. This results in a deviation from an optimal provisioning schedule, which is achievable in favourable years when resource levels and proximal conditions facilitate easy maintenance of the pair's body condition. In this system, any costs incurred whilst struggling to replenish or maintain adult body condition are passed on to the nestling. In a system where biparental care is necessary, incentive exists for

one partner to also act in a manner that facilitates the protection of the body condition of the other partner.

The nestling in turn may absorb such deviations from an optimal provisioning schedule in a manner that affects the development of temporary attributes, rather than fixed morphological attributes. This may be a testimony of the strong selective forces exerted by the ocean, which also discourages sexual dimorphism in pelagic seabirds. Reduced levels of provisioning recorded in less favourable years translated into lower average peak weights, smaller growth rates and however asymptotes reached generally did not differ significantly between years. However, the deviation from the optimal provisioning schedule during less favourable years may reduce the fitness of the fledgling, through a reduction in the post fledging buffer, including investment in a smaller post fledging fat deposits and decreased plumage quality. It is possible, that nestling shunt costs incurred away from skeletal or fixed attributes. The nestling once independent may overcome lower quality plumage and a smaller post fledging fat buffer, if conditions are favourable. Thereby, the offspring engages in its own risk minimisation strategy and makes the most of its only chance for survival.

Within a species, temporal patterns of parent provisioning and consequently foraging strategies are flexible. Firstly, a species may engage in a different foraging strategy ranging from unimodal to bimodal in response to prevailing conditions at a given location that affect the ability of adults to maintain their own body condition.

Consequently, even at the same location under different conditions a shift in foraging strategy may result. Secondly, an optimal provisioning schedule able to meet the needs of the nestling may only be realised during favourable conditions when a pair is



able to co-ordinate their efforts. The proportion of the colony able to achieve optimal provision is expected to vary between years and resource availability, as does the proportion of the breeding population able to return to the colony and lay an egg. Consequently, nestling quality of the cohort may be affected by the adult state dependent input system, based upon adult risk minimisation. This has implications for climate change, which affects sea surface temperatures and consequently oceanographic productivity and prevailing weather patterns.

Effectively, costs are passed on to the offspring whilst the reproductive potential of the adult or pair is maintained. Such flexibility allows iteroparous k-strategists, such as shearwaters, to persist successfully in areas of climatic and oceanographic variability, but may have implications on the post-fledging survival chances. In an adverse year, despite reaching lower average weights, a proportion of adults were still able to feed their nestlings to obesity, possibly highlighting differences in quality between pairs. Since the state of obesity reached and the quality of feather produced may translate into increased post-fledging survival chances for the nestling, the survival chances of nestlings produced by a breeding population may not be equal, as the level of parental care delivered may vary between pairs and years. The subtle adjustments in two tier adult state-dependent system of parental provisioning may alter the post-fledging survival chances of the cohort and this has implications on population dynamics in terms of climate change, which reach beyond easily observed reductions in breeding participation and success.

## **Dedication**

This thesis is dedicated to the dependable constants in my life:

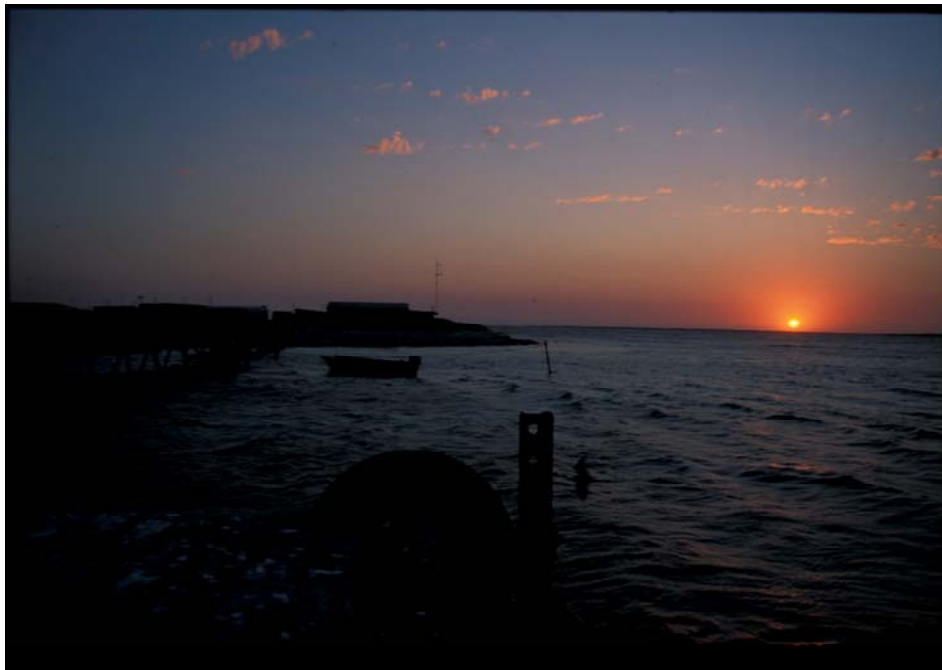
My parents and family, Ray Howarth, Bob Spence, the Mitchell – Armstrong family, Nic Dunlop, Mike Forde, gravity, seemingly eternal southerly winds, and the much anticipated, howling fronts which are preceded by periods of glassy splendour. A pattern that defines the cycle of life at the islands.

### **In memory of Ray who spent most of his life at sea.**

Thanks for all the laughs, fond memories  
and all the things I learnt from you, among them, that:

1. one should never listen to rumours... but to wait  
and form ones' own opinion.
2. fear is only a product of the mind.

### **Sail on glassy waters Ray**



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# 1 Chapter 1: Introduction

## 1.1 Overview and content

This thesis focuses on the parental care provided by two shearwater species, the winter breeding Little Shearwater *Puffinus assimilis tunneyi* and summer breeding Wedge-tailed Shearwater *Puffinus pacificus* along the Western Australian coast. The main focus of the study is the Little Shearwater as it is among the smallest of shearwater species and little is known about the subspecies breeding along the Western Australian coast. Research results will be utilised to comment on a potential two-tier model of parental provisioning which allows the persistence of a K-strategist in a relatively unstable environment. Potential implications on offspring viability are discussed, especially in regards to climate change.

Chapter 1 introduces the context of the thesis and key objectives (section 1.2), followed by a literature review to provide background information to aid in the interpretation of data and observed behaviour (sections 1.3 – 1.5). Here, the life history of shearwaters is discussed (section 1.3). The oceanographic environment is viewed in a broader context (section 1.4), as it ultimately shaped the life history and adaptations of pelagic seabirds over time. Reproductive activities observed cannot be separated from the oceanographic and climatic conditions consequently the environment in which the adults make their living is introduced. The variable oceanographic environment of the eastern Indian Ocean off the Western Australian is discussed in detail. This relatively unpredictable element is the dominant factor affecting food availability within an acceptable distance from the breeding colony and determines travel conditions.

Along the Western Australian coast the absence or presence of the warm tropical southwards flowing Leeuwin Current generates annual and inter-annual differences in sea surface temperatures, sea levels and local climate. The variable flow rate of the Leeuwin Current can only be understood in a global context and its apparent association with the southern oscillation index (SOI) are described. Global variations in climate affect oceanographic conditions and provide a relatively unpredictable influence on the regional and proximal environments, whilst seasonal changes are somewhat more predictable. The unpredictable changes in oceanographic conditions encountered during this thesis will be tracked, using an ongoing long term study of the reproductive performance of Wedge-tailed Shearwaters breeding along the Western Australian coast. This existing study will provide an index of regional oceanographic conditions to gauge the suitability of a given year to support shearwater reproduction. The annual life cycle of the two species is also placed into the context of predictable, seasonal changes in climate. The Little Shearwater *Puffinus assimilis tunneyi*, Wedge-tailed Shearwater *Puffinus pacificus* and their relatives are introduced with focus on functional attributes, breeding distribution and reference to existing research (section 1.5).

Chapter 2 introduces the methods used to conduct research in both species, whilst species specific methods are introduced in the relevant chapters. Chapters 3 to 5 focus on the Little Shearwater. Hatching and incubation is documented in Chapter 3, including an investigation of egg membrane composition using stable isotope analysis. Patterns of food delivery during the nestling period are examined in Chapter 4, whilst the results of the input system, in terms of growth of nestlings are

detailed in Chapter 5. The patterns of food delivery by the Wedge-tailed Shearwaters are detailed in Chapter 6, with some focus on seasonal changes in diet using stable isotope analysis. Chapter 7 focuses on the growth of Wedge-tailed Shearwater nestlings from hatching. Here respirometry was used to document basal metabolic rates and water loss of pre-fledging nestlings of variable feeding histories. Chapter 8 focuses on the behaviour of both species at sea using direct and indirect methods. Dive depths attained by Little Shearwaters were quantified using maximal depth gauges. Stable isotope analysis was used to investigate seasonal changes in diet using egg membranes and nestling plumage (Chapter 8), whilst egg membranes collected at different locations were also compared to view geographic and inter-specific differences in diet (Chapters 3 and 8). Finally, the application of this technique is evaluated and discussed in Chapter 9. In Chapter 9, results of the study are compiled and discussed. A tentative two-tier model of adult-state dependent co-ordination of parental care is presented, which leads to discussions focus on nestling viability, climate change and future research directions.

## **1.2 Context of the thesis**

Many studies of parental provisioning focused on pelagic procellariiformes have been conducted in the absence of reference to oceanographic conditions. However, the ability of an adult seabird to maintain its body condition is expected to change with oceanographic conditions. Consequently, resource levels are expected to limit reproductive participation and success, potentially define the quality of participants, and also influence the overall ability of a colony to provide for their offspring. The Western Australian coast provides a suitable place to study adult behaviour in the context of oceanographic conditions, given the inter and intra annual fluctuations in

oceanic conditions experienced as a result of variations in the strength of the Leeuwin Current, whose rate of flow is determined by global climatic events (section 1.4.4). Here, variations in climatic conditions have been found to affect both the breeding participation and success of summer breeding tropical seabirds, especially that of the Wedge-tailed Shearwater (Wooller et al. 1991, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006) (section 1.4.5). Although, no three-year study can explore the trends in seabird reproduction in relation to such factors, the existence of an ongoing long-term study of Wedge-tailed Shearwaters provided an index of oceanographic resource levels and allowed the interpretation of findings within a wider context.

Fortunately, this study encompassed one year of strong current flow (2000), one transitional year (2001) and a year (2002) associated with weak Leeuwin Current flow when cooler waters prevailed offshore. In addition to easily measured outcomes such as reproductive participation, failure or success, which have been monitored in other studies on the Western Australian coast (Wooller et al. 1991, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006), more subtle effects of climate upon parental provisioning were investigated – such as nestling weights which reflect the adults ability to provide food. The expansion of existing work will increase our understanding of potential mechanisms, the effects of climate change on seabirds and may help to explain the southwards range expansion documented for several species of tropical seabirds along the Western Australian coast (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001, Bancroft et al. 2004)



Traditional models denote that long-lived K-strategists reproduce in stable conditions. The oceanographic variability recorded along the Western Australian coast, suggests that seabirds reproduce in unstable conditions. This study will comment upon life-history strategies of long-lived seabirds and their successful radiation in relatively unstable and unpredictable environments. The level of parental care provided by the K-strategist during variable oceanographic conditions will be investigated, especially the amount and frequency of food delivered, whilst also focusing on constraints which may affect parents, including adult body weight, immediate weather and regional oceanographic conditions.

The interaction between seabird provisioning and immediate weather conditions will be examined. Obviously, seasonality has a predictable effect upon the weather patterns experienced along the Western Australian coast. Whilst, the variable flow of the Leeuwin Current between different years has the potential to produce subtle inter-annual variations in climate. During years when the warm Leeuwin Current flows strongly in autumn elevated sea surface temperatures are maintained which sustain active or dissipating tropical cyclones for longer, and provide opportunity for such system to travel to higher latitudes. The effect of dissipating tropical cyclones on the relatively broad-winged Wedge-tailed Shearwater provisioning will be examined during the study. Given the species tropical breeding distribution and comparatively broad wings it is expected to be relatively tolerant of low wind conditions. Similarly, the study will examine the interaction between the weather experienced in winter and Little Shearwater provisioning patterns. The southern breeding distribution of the Little Shearwater and its comparatively narrow wings suggest it is a species suited for

high wind conditions. Weather systems have the potential to alter travel costs, given that pelagic seabirds often utilise them for locomotion.

Traditionally, studies of parental provisioning and nestling obesity in Procellariiformes have focused on species breeding at higher latitudes or dependent on distant high latitude resources that are temporally limited as a result of predictable seasonality (1.3.3). Following the sharp seasonal decline of high latitude resources many of these species undergo trans-equatorial migrations and often nestling obesity and a period of nestling desertion was recorded (Warham 1990; Warham 1996). Less research has focused on species breeding at lower latitudes. In this study at approximately 30 ° latitudes it was expected that nestlings would not be deserted before fledging. If obesity served to overcome a period of pre-fledging desertion associated with a seasonal decline in resources it should not occur at mid latitudes, where seabird reproduction occurs in both winter and summer indicative of ongoing resource availability.

Obesity has also been proposed to be a by product of chronic overfeeding in the absence of a reliable feedback mechanism (section 1.3.2 and 1.3.3). Literature suggests that both species feed their nestlings regularly and are therefore expected to have sufficient opportunity to obtain feedback about nestling condition, which should prevent chronic overfeeding and resultant obesity. Consequently, obesity is not expected to occur in either species. Respirometry and supplementary feeding of Wedge-tailed Shearwaters will be used to investigate aspects of parental provisioning and pre-fledging weight loss to supplement the field data collected.

The breeding biology of the Little Shearwater has not been extensively examined at a subtropical location in the southern hemisphere. Results will contribute towards the understanding of seabird biology along Western Australian coast and serve as a comparison to existing studies of the species at other locations. The Little Shearwater is the smallest shearwater (Harrison 1985) and is therefore expected to have a higher resting metabolic rate and its threshold weight would be reached after a smaller weight loss than in larger species. This suggests that the Little Shearwater is an ideal species in which to study parental behaviour, especially how the ability to maintain adult body condition may affect continuity of parental care during incubation and nestling feeding.

Little is known about the foraging behaviour of the Little Shearwater breeding at lower latitudes of the Western Australian coast. Common belief prevails that its foraging was likely to be size restricted and it was predicted that it would forage near the breeding sites. The distribution of the Little Shearwater suggests that it is adapted to forage in cold water, whereas Wedge-tailed Shearwaters are associated solely with tropical waters. Based upon observations of birds in association with sea surface temperatures (Brooke 2004) it may be deduced that Little Shearwaters are more likely to excel in years of reduced sea surface temperatures or forage in zones dominated by cool water. Zones of cooler water are often found inshore along the Western Australian coast, where a northwards flowing counter current exists (Pearce 1997). Given its southern distribution of the Little Shearwater, it was also thought that the species was more likely to forage in cool inshore shelf waters. Opportunistic voyages on fishing and charter vessels and feedback from the skilled observers during the Little Shearwater breeding season will be used to locate Little Shearwaters at sea.

Observations of seabirds at sea provide an insight into the foraging behaviour of adults at sea. It however is often difficult and time consuming to collect direct observations at sea. Consequently, indirect methods of approximating adult behaviour at sea were employed. Since, little was known about dive depths in Little Shearwaters maximal depth gauges were utilised to examine foraging behaviour during incubation and nestling feeding. The potential use of stable isotope analysis to elucidate the behaviour of pelagic seabirds at sea will also be examined.

Stable isotope analysis focuses on the time specific materials, such as egg membranes and nestling plumage to comment on foraging behaviour (Bearhop et al. 2001). Here materials will be used to draw comparison between species engaged in similar behaviours and within a species at different locations and times in the breeding season. The technique was used to question the ability to directly compare the mass of food delivered to nestlings over time, as composition of meals may change in terms of energy and nutritional values with seasonal changes in diet. Nonetheless, meal sizes based on mass alone are often directly compared in seabird research, including meal sizes delivered within a species over time, between different locations and between subspecies and between species. Stable isotope analysis will be used to detect potential changes in diet with season in Wedge-tailed Shearwaters. The potential applications of this indirect technique will be examined with focus on its ability to track the changing behaviour of adults at sea, that can otherwise be time consuming to understand.

### 1.3 Environmental pressures and life history strategies

Pelagic seabirds, such as shearwaters spend most of their life at sea, riding the winds generated by the mobile weather systems generated by mobile masses of water of different sea surface temperatures, whilst searching for spatially scarce resources.

Visits to land are generally confined to breeding attempts at breeding colonies.

Anatomical adaptations to the dominant environment allow shearwaters to move with skill in the air and water, whilst on land they appear cumbersome (Warham 1996, Spear and Ainley 1997a, 1997b). In *Puffinus* species, sexual dimorphism is small (Warham 1990), suggesting that the need to maintain an optimal performance in the oceanographic environment may exert strong, stabilising selective forces (Bull 2004).

Pelagic seabirds have incredibly large home ranges and are only tied to a central location when adults raise a dependent offspring cached at the breeding colony.

During reproduction, sufficient resources must be transported from often distant foraging locations to a central breeding site until their progeny are able to join the population at sea. Since seabirds are often colonial breeders, the resources needed by a colony are large and competition will arise between pairs (Brooke 2004). The accumulation of food and subsequently excreta has implications for the nutrient dynamics of island and surrounding marine ecosystems (Anderson and Polis 1998).

Adaptations displayed by shearwaters are also suggestive of energy conservation.

Large distances are covered with minimal flight costs through the use of dynamic soaring (Warham 1996, Shealer 2002, Brooke 2004). Heat loss is often reduced by insulating, subdermal fat stores, which can be metabolised. Species which travel

large distances between foraging and nesting sites often produce low weight, high-energy stomach oil, which can be fed to nestlings or metabolised according to need. The stomach oils maximises energy delivery to the dependent nestling from a distant foraging location while minimising pay loads and flight costs experienced by the adult during travel (Warham 1990). Such adaptations has allowed pelagic Procellariiforms to thrive in oceanographic environments often thought to be unstable and ephemeral, with resources scattered over large areas (Lack 1968, Ashmole 1971).

The oceanic environment also exerts strong selective forces on life-histories, which are extreme and diverse in seabirds (Richdale 1957, Lack 1968, Ashmole 1971, Ricklefs 1990). Life-histories describe the journey of organisms from conception to death, including age of first reproduction and reproductive life span (Stearns 1992). Seabirds, such as shearwaters, are generally characterised by life-history traits often associated with long-lived iteroparous species, such as delayed maturity, low reproductive rate, slowly developing young, long reproductive life span and high adult survival (Warham 1990, Brooke 2004).

Shearwaters belong to the order Procellariiformes, which also includes albatrosses and petrels. Over a hundred species in the Procellariiformes are able to gather energy from the ocean in different manners as reflected in their differences in size, flight attributes, foraging technique and diet (Warham 1990, 1996, Brooke 2004).

Nevertheless, despite their successful radiation, Procellariiformes display a convergence in reproductive traits. Procellariiformes are generally colonial breeders, which lay only a single, energetically expensive egg during each breeding attempt. It is rare for them to replace a failed egg (Warham 1990). The development of their

nestling is slow compared to similar sized land birds, as evident in the prolonged incubation and nestling period (Warham 1990, Brooke 2004). Consequently, adults invest more time and energy in reproduction than most birds. This investment is amplified when nestlings attain body weights in excess of adult body weight, which must be lost before fledging (Serventy et al. 1971, Warham 1990, Brooke 2004). Naturally, there has been much speculation as to why adults would allocate precious resources and time to over feed their nestlings to an apparent state of “obesity”, especially when their other adaptations are suggestive of energy frugality.

This study investigates parental provisioning in shearwaters, particularly how the parents provide heat, food and protection from predation for the offspring. Since birds lay eggs, gestation occurs outside the thermoneutral zone of the female body conducive for metabolism, cell division, growth and development of the young. Iteroparity introduces the need to incubate the egg, decrease pay loads to females during flight, and also introduces the ability to “desert” a breeding attempt during adverse conditions. Shearwaters dig a burrow to cache their single offspring, and the burrow provides a buffered microclimate. Nonetheless, eggs need incubation, and both egg and hatchlings are susceptible to predation. Biparental care is normal, although tasks may not be divided equally temporally between parents (Booth et al. 2000, Gray and Hamer 2001). From an energetic perspective equal sharing of labour may occur, since the female invests more energy to form the egg, whilst the male may guard the burrow before an egg is laid or play a larger role during incubation of the egg, whilst the female forages to replenish body resources (Brooke 2004).

Whilst in the egg, the offspring is dependent upon the resources deposited into the egg by the female before laying. Once hatched, the nestling is totally dependent upon the efficiency of the food delivery system orchestrated by the parents to support its transition into a functional free-flying young adult. In shearwaters biparental care is generally required to successfully raise a nestling (Warham 1990, 1996). During each breeding attempt, it would therefore be advantageous for one partner to structure its investment to maintain the body condition of its other partner. Reproductive success in procellariiformes generally increases with the duration of a pair bond, suggesting that lifetime reproductive success is maximised by mate fidelity (Brooke 2004).

Trade-offs are made when finite resources, including time and energy, are allocated differently to conflicting uses on an optimal basis determined by selective pressures (McFarland 1993). Commitment of resources to one trait or stage is associated with costs, which may directly or indirectly impair the development of other traits and block mutually exclusive opportunities (Trivers 1972, Krebs and Davies 1990). Costs and benefits can be viewed on various time scales, but ultimately benefits are measured in terms of fitness. Over time selection is expected to support optimal allocation of resources and development of traits. Life-histories, like morphology, should be shaped by the summation of evolutionary forces, and may be a testimony of what has worked best for a species in the past, and most are relatively fixed. The choices made by individuals during a life-time, or the strategies adopted by individuals, introduce flexibility to the system and introduce opportunity for refinement and reaction to environmental conditions. Those that excel in making appropriate choices will produce more viable offspring during their lifetime. Once



the whole population adopts a pattern of behaviour, it can be viewed as an evolutionarily stable strategy (Stearns 1992), which may ultimately become an innate trait.

For reproduction to be successful, the pair advances through several phases during each of which adults may choose to withhold further allocation of resources.

However, with time investment in the current reproductive attempt accumulates and it becomes more costly for the pair to terminate the attempt. Firstly, pairs must form and decide whether to participate in a given reproductive season, a decision that is greatly influenced by past allocation of resources. Reproduction is only possible if a certain body condition has been reached (Chastel 1995) and plumage condition is optimal. In pelagic seabirds functional flight feathers are generally grown outside the reproductive season. It is expensive in terms of energy and resources to grow new feathers, furthermore during the moult, flight and foraging performance are impaired (Warham 1990; Warham 1996). When providing for a dependent nestling, flight and diving performance should be optimal. Indeed, foraging ability may be highly dependent upon plumage condition, since seabirds often cover large distances between dynamic foraging and fixed breeding sites, whilst carrying extra pay loads to feed the dependent offspring (Warham 1990). Secondly, adults may withhold further incubation effort, or delay food delivery to the nestling, even at an advanced stage of the breeding attempt when resources investment is high. Hence, in a given year, not all of the potential breeding population may be engaged in reproduction and environmental conditions may reflect the quality of participants. Generally, one would expect many adults to breed in favourable years, but for there to be limited participants during less favourable years.

During each breeding attempt, long-lived birds with low annual fecundity and late sexual maturity are expected to favour preservation of breeding adults, at the expense of the survival chances of the current progeny, which may or may not survive to breed. Thereby, adults have a greater chance of surviving to breed in future years and this strategy facilitates low adult mortality and a long reproductive life span. Adults have been shown to protect body condition at the expense of the nestling in Leach's Storm Petrel *Oceanodroma leucorhoa* (Mauck et al. 1995, Takahashi et al. 1999b), Antarctic Petrel *Thalassoica antarctica* (Tveraa et al. 1998) and the Yellow-nosed Albatross *Diomedea chlororhynchos* (Weimerskirch et al. 2000). However, reproductive output and the set of decision rules may vary with the age and history of individuals in relation to their total reproductive lifespan (Stearns 1992). Life-time reproductive success is difficult to document for long-lived species, but has been summarised for the Short-tailed Shearwater *Puffinus tenuirostris* (Wooller et al. 1990, Wooller et al. 2003). In Australia, Short-tailed Shearwater reproduction is supported by large energy influxes from Antarctica, where adults forage during long absences from breeding grounds (Klomp and Schultz 2000).

The breeding efforts of long-lived seabirds are supported by ephemeral, fluctuating oceanographic conditions, especially off the Western Australian coast where no major, stable upwellings are known to occur (Wooller et al. 1991). Traditional K-strategist models are suited for stable conditions (Krebs and Davies 1990), but evidently long-lived organisms, such as seabirds, can also cope with potentially unstable conditions. As an additional strategy, bet-hedging may occur when

selection favours the allocation of resources away from those stages in the life-cycle that carry the greatest risks or uncertainties (Wooller et al. 2003).

Bet-hedging provides another model for the evolution of a long life-span, alternative to the K-strategist model, which is based on stability. In the bet-hedge model, unpredictable resources favour a reduction in the number of young per attempt and an increase in the number of attempts, which also results in a long life span (Wooller et al. 2003). Bet-hedging adults will attempt reproduction whenever possible in anticipation of adequate resource levels to facilitate success. During bad years, which are frequent in erratic environments, reproductive success drops, but some, usually experienced, adults will still be able to produce comparatively valuable young. Procellariiformes, such as Short-tailed Shearwaters fit this model, as they lay a single egg, have a long reproductive lifespan and the population displays marked annual variability in reproductive success. Overall, bet-hedging can be used to explain the persistence and evolution of long-lived organisms in unstable environments, such as those characteristic of the ancient, nutrient-poor Australian continent and the oceans of the world (Wooller et al. 2003).

### 1.3.1 Why study parental provisioning?

Parental provisioning examines the tension between the functional adults, which has reached reproductive potential, and the potential progeny that could ultimately ensure the temporal persistence of related genes (Stearns 1992). The altricial nestling is totally dependent upon the adults for survival. Parental provisioning is a long process, stretching from the pre-laying period to fledging. Initially, adults have to be in a condition to resume reproduction, attract and defend a good partner, claim, build

and defend a burrow in which to raise the nestling. Then, female foraging at sea determines the reserves deposited in the single large egg. Thereafter, biparental care is needed to maintain the egg at a temperature that supports growth and development of the embryo within. Hatching is followed by a relatively brief brooding phase. After this, adults only return to the colony at night to feed the nestling to fuel its development into a functional fledging. It has been documented that more experienced and higher quality pairs lay larger eggs (Amundsen et al. 1996) whose nestlings also grow faster (Weidinger 1996). Adults may at any stage of the process terminate the breeding attempt (Warham 1990), being a state-dependent activity (McNamara and Houston 1996). Whilst studying parental provisioning one can only access the reproductively active proportion of the breeding population in any given year.

In birds, traditionally clutch size was thought to settle at an optimum size or the Lack clutch size that produces most fledglings. Parents would prefer to start with a maximal clutch size and selectively cull, according to proximate factors, to arrive at an optimal clutch size that ultimately maximises adult life-time reproductive success. In contrast, individual nestlings should selfishly favour a small clutch size, which promises maximal levels of provisioning and promotes their survival. Systems studying the interaction of both parental and offspring genes would be best analysed as an evolutionarily stable strategy (Stearns 1992). The single egg, characteristic of Procellariiformes, appears to be the product of some lineage-specific effects and, as a result, it eliminates trade-offs between clutch size and brood size (Stearns 1992). Consequently, the two species of *Puffinus* shearwaters selected for the study make an ideal model to study parental provisioning.

### 1.3.2 Theories of nestling obesity

Nestling obesity, approaching up to 170% adult weight, appears to be universal in Procellariiformes (Warham 1990). The prevalence of nestling obesity suggests it endows an obscure evolutionary advantage, which exceeds the direct costs, in terms of energy delivered by the adults. As a result, a plethora of hypotheses have been proposed to explain nestling obesity. These view obesity from a combination of different angles, explaining it to be a product of the environment, a product of internal events within the adult or nestling or a manifestation of a foraging strategy and the resultant feedback mechanism between the nestling and the adult. Potential mechanisms that may control food delivered by the adults to the nestling are discussed in section 1.3.3. Here the feedback mechanism is examined, which has thought to result in nestling obesity and also introduces the importance of adult body condition.

It seemed plausible that the nestlings should be buffered against the temporally and spatially patchy distribution of oceanic resources, which ultimately affects energy flow into the breeding population (Lack 1968, Ashmole 1971). In birds adapted for starvation physiology, a lipid buffer could be metabolised during prolonged periods of fasting during reduced provisioning. Unfortunately, subsequent studies demonstrated that the amount of excess weight carried exceeded disruptions in provisioning (Ricklefs et al. 1985, Hamer and Hill 1993, Bolton 1995, Hamer and Hill 1997). It was then suggested that nestling obesity might be a buffer against individual differences in foraging success, rather than against fluctuations experienced by a

colony as a whole (Ricklefs and Shew 1994), reducing the impact of chronic stochastic delivery of food upon individual nestlings (Hamer and Hill 1997).

Other hypotheses presented focus on events within the developing nestling. Nestling obesity may be a by-product of nutrient limitations (Ricklefs et al. 1980). Conversely, catabolism of previously deposited adipose tissue by nestlings may serve to support an energy-expensive growth phase, such as the growth of flight feathers (Reid et al. 2000). Although, nestlings lose weight before fledging near adult weight, lipid reserves may provide a consumable, lightweight buffer after they become free-flying fledging (Reid et al. 2000) and in some species heavier fledglings have higher survival rates (Sagar and Horning 1998). These more nestling-orientated functions for obesity would allow adults to produce nestlings of variable quality and with a fitness potential largely dependent upon the level of parental provisioning attainable by the adult pair.

### 1.3.3 Control of food delivery to the nestling

Several studies have explored how food delivery is controlled, if the adults are able to react to the state of the nestling, conveyed both as a visual cue and by its begging behaviour. Some species did not adjust food delivery in relation to the age, size or nutritional status of the nestling (Ricklefs et al. 1985, Ricklefs 1990, Ricklefs 1992, Hamer 1994). Since, most species studied do not feed their nestlings regularly, this was thought to reflect the absence of a reliable feedback mechanism, which would favour “chronic overfeeding” (Ricklefs 1990, Ricklefs and Shew 1994). Conversely, other species that feed their nestlings regularly appear able to adjust provisioning in accordance with nestling needs (Bolton 1995, Hamer and Hill 1997, Hamer et al.

1998, Granadeiro et al. 1999, Hamer et al. 1999, Baduini 2000). An interaction was thought to exist between the foraging strategy employed and the ability of adults to react to nestling needs.

Reliable feedback about the state of the nestling is dependent upon the temporal interval at which adults visit the nest (Ricklefs 1992, Ricklefs and Shew 1994, Hamer and Hill 1997, Hamer and Thompson 1997). In species that engage in a bimodal foraging strategy, alternating short and long absences, the opportunity for reliable feedback is reduced during long absences. For example, birds such as Short-tailed Shearwaters often cover distances of 15 000 km during absences lasting up to 21 days (Klomp and Schultz 2000). At the other end of the continuum, some species feed their nestlings nearly every night, and are faced frequently with a potentially reliable feedback mechanism and are able to adjust provisioning rates accordingly. For example, Wedge-tailed Shearwaters, using a unimodal foraging strategy, food delivery was inversely proportional to nestling nutritional status, yet still directly proportional to parental nutritional status (Baduini 2000). However, a clear picture does not emerge, as the Yellow-nosed Albatross uses a bimodal foraging strategy, but can regulate provisioning to suit the needs of the nestling (Weimerskirch and Guionnet 2002). A co-ordinated dual foraging strategy has been recorded for the Little Shearwater in New Zealand, and introduces a new dimension to parental provisioning in Procellariiformes. Here, despite regular feedback and nearly daily delivery of food, nestlings were still overfed (Booth et al. 2000b). However, at other locations the Little Shearwater has not been recorded to co-ordinate foraging efforts (Hamer 1994), although nestlings were fed nearly every night (Hamer 1994, Priddel et al. 2003) and obesity was reached (Hamer 1994, Priddel et al. 2003).

Often, in Procellariiformes, a dual foraging strategy appears to be employed to maintain adult body condition above a certain threshold, whilst supporting reproductive events at a central location. During short absences, the nestling is fed at a high rate, but it appears as if self-feeding by adults during short absences is negligible and adult body conditions depleted (Weimerskirch 1995, Weimerskirch et al. 2003). Conversely, during long absences, adult body conditions improved in the Blue Petrel *Halobaena caerulea*: (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 2003), Wandering Albatross *Diomedea exulans* (Weimerskirch 1995), Sooty Shearwater *Puffinus griseus* (Weimerskirch et al. 1994, Weimerskirch 1998) and Short-tailed Shearwater (Klomp and Schultz 2000). This highlights the underlying aim of long-lived organisms to maintain adult survival and reproductive potential (Weimerskirch et al. 1994).

Indeed, several species have been documented to use their own body condition as a basis to regulate investment rates at the expense of the nestling (Muck and Grubb 1995, Tveraa et al. 1998, Takahashi et al. 1999b, Weimerskirch et al. 2000).

Theoretically, a fixed level of investment means that an adult will deliver food in accordance with its own intrinsic rhythm, generally independent of the needs of the nestling or its partner, in order to favour its own future reproductive success (Ricklefs 1987, 1992, Hamer and Hill 1993, Lorentsen 1996). Under such circumstances, “chronic overfeeding” would protect the nestling from chance starvation (Ricklefs 1990, Ricklefs and Shew 1994). There is some evidence that adults do not respond to increased needs at the nest (Ricklefs 1992, Hamer 1994, Muck and Grubb 1995, Hamer et al. 1999) and differences in findings may rest upon the ability to gain



reliable feed back on nestling conditions during long absences (Ricklefs 1992). However, adult response has not been coupled with an index of oceanographic conditions.

Alternatively, some studies suggest that investments are flexible in accordance with the needs of the nestling (Johnsen et al. 1994, Bolton 1995, Bertram et al. 1996). Generally nestlings in poor condition were fed more than ones in good condition in Cory's Shearwaters *Calonectris diomedea* (Granadeiro et al. 1999) and Wedge-tailed Shearwaters (Baduini 2002). However, the Manx Shearwaters *Puffinus puffinus* reduced feeding rates in accordance with the begging intensity of large nestlings, but did not increase food delivery to poorly fed nestlings (Hamer et al. 1999). Such outcomes suggest that parental provisioning should also consider adult condition (Weimerskirch 1995, Lorentsen 1996, Takahashi et al. 1999, Weimerskirch et al. 1999, Takahashi et al. 1999b). It is easy to reduce provisioning, but only adults in good condition may be able to increase provisioning in response to increased demands at the nest (McNamara and Houston 1996, Erikstad et al. 1998). It appeared as if adults in poor condition could not increase food delivery without falling below a threshold weight and potentially endangering their own reproductive potential (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 1994). Thus, food delivery appears to be adjusted in accordance to nestling needs and adult body condition, such that the ability of the adult to respond to nestling needs ultimately rests upon adult body condition (Muck and Grubb 1995, Tveraa et al. 1998, Takahashi et al. 1999b, Weimerskirch et al. 2000). In turn, adult body condition relies heavily upon oceanographic conditions.

## 1.4 Adult shearwaters and their environment

This chapter highlights some characteristics of the physical environment of seabirds breeding along the Western Australian coast, including the influence exerted on seabird reproduction by the Leeuwin Current, which may vary in strength between years (Pearce and Walker 1991, Pearce 1997). Species breeding along the Western Australian coast are influenced by relatively predictable seasonal changes in climate (section 1.4.1), and such predictable events have the potential to shape annual life histories and distribution (section 1.4.2). However, seabirds also face unpredictable changes in conditions as a result of the variability of the flow rate of the Leeuwin Current, which are linked to global climatic events and ultimately alter local climate and oceanic resource levels between years. The relatively unpredictable variations in the flow rate of the Leeuwin Current (section 1.4.3) are linked to the southern oscillation index, which also provides a measure of global climatic conditions. Resultant differences in oceanographic conditions owing to changes in global climatic conditions have been demonstrated to effect seabird breeding participation and reproductive success along the Western Australian coast (section 1.4.4). In this study it was possible to investigate shearwater provisioning under variable conditions to provide insight into a potential mechanism in which reproduction at a central location may be affected by changes in climatic conditions.

To seabirds, the thermal state of the ocean is of primary importance. Seasonal changes in sea surface temperature effects seabird distribution (sections 1.4.2 and 1.4.5). Seabirds ride the winds generated by weather patterns and feed at zones of productivity. Effectively, their whole world is driven by the influence of the sun's heat on the earth's surface (Lawrance 1986, Colls and Whitaker 2001). Above the

surface of the differentially heated earth, circulation patterns and weather systems are generated, which birds use for locomotion. Generally, differences in thermal state dictate wind strength and direction which influence energy efficiency of locomotion in pelagic seabirds (section 1.4.5). Whilst, the interaction of thermally disparate water masses, catalyse areas of food production (Warham 1990; Brooke 2004). Water is also a mobile medium that gives rise to ocean currents, which transport water of different properties. The thermal states of the mobile water masses have ramifications upon their density and salinity, with tropical water being less dense and more saline than cold water. When disparate water masses interact, upwellings or other features associated with productivity can result (Brooke 2004).

The rotation of the earth allows mobile disparate water masses and the associated weather systems to travel around the world in an easterly direction and determine the world which pelagic seabirds inhabit, especially in the southern hemisphere. The winds flowing along pressure gradients between different weather systems are used by foraging seabirds to travel economically, since dynamic soaring makes use of the winds deflected from a dynamic landscape composed of waves that can deflect winds and generate updrafts.

#### 1.4.1 Seasonality and local climate

Each species was studied at a different time of the year, when predictable seasonal differences in climate persist. Furthermore, the study was conducted at different locations along the Western Australian coast, located at different latitudes and at different distances from the mainland. Seasonal differences in climate are generated

when the earth travels around the sun resulting in differential heating of each hemisphere. Such seasonal differences are amplified at high latitudes, as the poles are engulfed in darkness for a period of time each year and remain cold. In the austral winter, the sun's impact is more direct than in the southern hemisphere and shifts the equatorial convergence to the northern hemisphere (Lawrance 1986, Colls and Whitaker 2001). Consequently, all circulation cells shift in latitude in accordance to heating. This pronounced seasonal shift in latitude of circulation cells and associated weather systems largely accounts for seasonal variations in climate experienced within a year (Table 1.1a). For example, when the circulation cells shift northwards in winter, the rain bearing fronts, which travel at higher latitudes in summer, finally reach the Western Australian coast.

In the austral summer, the sun heats more of the southern hemisphere. Therefore, the meteorological equator, associated circulation cells and generated, predictable pressure belts shift southward. During this time, the cyclonic activity shifts southwards and northern Australia is affected by tropical cyclones (intense tropical low pressure systems) and summer rains (Lawrance 1986, Colls and Whitaker 2001). Occasionally tropical cyclones will travel down the coast as far as Exmouth, sending large rain-bearing depressions further south, along an inland (south east) path and only occasionally south along the west coast. Thus, only infrequently do the coastal areas south of Carnarvon receive summer rains. In summer, the areas of high pressure cells which travel around the southern hemisphere are located over the south west to mid west coast of Western Australia. These generate the characteristically strong southerly winds. As the Antarctic region is bathed in sunlight, the bands of low pressure systems that circle the southern hemisphere travel at higher latitudes are

**Table 1.1** The annual timing of shearwater breeding events and weather experienced on the Western Australian coast.

less intense and seasonal food-webs form at the subantarctic convergence.

Seasonality and the associated movement of sunshine and food resources influence seabird distribution and breeding activity (Brooke 2004). In the higher latitudes of the southern hemisphere, breeding generally occurs during the austral summer, with most seabirds departing to lower latitudes in winter. Many species are seen as winter visitors in waters off the mid-west coast of Western Australia, including the Fleshy-footed Shearwater *Puffinus carneipes*, Great Skua *Catharacta skua*, Yellow-nosed Albatross, Cape Pigeon *Daption capense*, Southern Giant Petrel *Macronectes giganteus*, Australasian Gannet *Morus serrator* and prion species *Pachyptila spp.* Some summer breeders at the study sites depart and travel still further north in winter, such as the Common Noddy *Anous stolidus*, Lesser Noddy *Anous tenuirostris*, Sooty Tern *Sterna fuscata* and Bridled Tern *Sterna anaethetus*. The sites visited during the non-breeding season, ultimately determine the ability of seabirds to participate in future reproductive events, and therefore influence the proportion of the colony encountered by researchers at the breeding site. Therefore, the variability in oceanographic resources experienced along the Western Australian coast may have far reaching influences on reproductive participation of seabirds breeding at higher latitudes, including the Fleshy-footed Shearwater, which breeds on islands off the south-western Australian coast.

The climate experienced at each site was also influenced by latitude. In winter, locations further north are dominated by a belt of large high pressure cells and experience higher ambient temperatures and lower winter rainfall whilst the effects of the cold fronts are reduced, compared to the south west. Furthermore, the continent

heats up more at lower latitudes, resulting in greater pressure difference and stronger winds within the belt of high pressure cells. Generally, the wind speed of the winds associated with the high pressure cells, increase from south to north.

The local climate experienced at the study sites was also influenced by their proximity to a large, heat-labile landmass, such as the Australian continent. The Houtman Abrolhos Islands are a collection of small, low islands that are located 55 to 110 km off the coast. Here the mainland has less ability to influence local weather and the Houtman Abrolhos Islands often experience more oceanographic weather as dictated by the eastward passage of differential pressure cells, however some influence of the mainland is felt (Pearce 1997). In contrast, Rottnest and Lancelin Islands are located within 20 km and 1 km respectively near the coast and the weather experienced at is strongly influenced by their closer proximity to an immense continent, which affects both winds and temperatures. At night, the land cools more rapidly than the ocean so that air sinks over the land and picks up heat to rise over the ocean, which sets up a localised circulation with offshore winds prevailing on the surface. Such localised winds generated by the different thermal properties of the ocean and land are not always experienced at the Abrolhos Islands, where often periods of uninterrupted howling southerly winds prevail. During the day, especially in summer, when the continent heats up and air rises above it, more air is drawn in from the ocean to replace it. In Perth, this adiabatic effect is called the “Fremantle doctor”.

Wedge-tailed Shearwaters engages in the main breeding activities from October to May, whilst the Little Shearwater breeds from May to December. Therefore seasonal differences in climate are experienced. In a given month, as a result of latitude and

proximity to a large land mass the winds experienced at each study site also varied in both direction and magnitude. Wind roses are presented for North Island in the Wallabi Group of the Houtman Abrolhos Islands (Figure 1.1), Lancelin Island (Figure 1.2) and Rottnest Island (Figure 1.3) depicting average conditions experienced during the research. However, given the difference in weather experienced in El Niño and La Niña years it is questionable if they should be averaged, and in the future typical weather for each extreme may be available.

#### 1.4.2 Sea surface temperatures and seabird distribution

The species richness and abundance of procellariiforms increases with latitude (Chown et al. 1998). High latitudes are associated with predictable and seasonally high productivity, although only seasonally sunlit (Brooke 2004). Seabird distribution, especially that of petrels, has been linked to sea surface temperatures (SSTs) which affect temperature, salinity and often turbidity of water (Warham 1996, Shealer 2002, Brooke 2004). For example, the Wedge-tailed Shearwater and Audubon's Shearwater *Puffinus lherminieri*, are associated with warm water, whereas the Short-tailed Shearwater Shearwaters and Fleshy-footed Shearwater occur over cold water (Warham 1996). Some species focus on narrow bands of sea surface temperatures and salinity, while others adopt a more generalist strategy (Hunt et al. 1992). Wedge-tailed Shearwaters are most abundant in waters above 21 °C and associated with salinity values of 34.6 ppm, but tolerate a range of SST and salinities (King 1955, Dunlop and Wooller 1990).



**Figure 1.1** Wind roses for North Island at the Houtman Abrolhos Islands prepared by the Bureau of Meteorology, using available data for 2000 to 2002.

**Figure 1.2** Wind roses for Lancelin prepared by the Bureau of Meteorology, using available data for 2001.

**Figure 1.3.** Wind roses for Rottnest Island prepared by the Bureau of Meteorology, using available data for 2002.

The link between seabird abundance, latitude and SSTs is also apparent along the Western Australian coast. Off the south-western Australian coasts, the petrel and albatross assemblages encountered increased in abundance and diversity where two fingers of cooler low-density water swept close to the coast (Surman and Wooller 2000). Wedge-tailed Shearwaters have been observed along the Western Australian coast north of Cape Leeuwin at a mean sea surface temperature of 20.9 °C, a mean salinity of 35.82 ppm and over a mean water depth of 1586m. Wedge-tailed Shearwaters are rarely seen in waters south of Cape Naturaliste, where they are replaced by Fleshy-footed Shearwaters (Surman and Wooller 2000), which breed on islands off the southern coast.

In contrast, Little Shearwaters are rarely seen on voyages along the coast despite breeding on many offshore islands. Published observations of Little Shearwaters at sea are rare, and some unpublished observations by Dr Chris Surman and Dr Nic Dunlop will be presented in Chapter 8. Published observations, for the Western Australian coast, appear to be restricted to one Little Shearwater observed near Cape Naturaliste at sea surface temperatures of 17.7 °C and salinities of 35.88 ppm and at a water depth of 70 m (Surman and Wooller 2000). This is in keeping with known distribution and suggests that the Little Shearwater is most suited for cold waters. Nonetheless, Little Shearwaters breed at lower latitudes off the central west coast, albeit in winter, and must forage nearby, since nestlings are fed nearly daily.

El Niño Southern Oscillation (ENSO) events are associated with different SSTs and will invariably affect seabird foraging and reproduction. For example, oceanic productivity may be affected, or events may be shifted to locations too far from

breeding sites to make reproduction viable (Warham 1996, Brooke 2004). Climate change and associated changes in oceanographic conditions are therefore a direct threat to seabirds, and can greatly influence reproduction (Cruz and Cruz 1990). The foraging success of Wedge-tailed Shearwaters appears to be directly influenced by daily changes in SSTs, which ultimately affect breeding success (Peck and Congdon 2003, Smithers et al. 2003). SSTs are directly influenced by climate and, at the Western Australian coast, by variations in the strength of the Leeuwin Current. Here, a southwards range extension has been documented for several tropical species of seabirds (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001, Bancroft et al. 2004), signalling that conditions are changing along the Western Australian coast.

#### 1.4.3 The Leeuwin Current and the Southern Oscillation Index (SOI)

All other western seaboard in the southern hemisphere experience north-flowing, cold water currents. At other continents areas of north-flowing cold currents are associated with large upwellings, which bring nutrients into the surface photic zone and thereby enhance the primary productivity upon which food chains rest. Evidently within the Indian Ocean a northwards circulation cell exists, generated when eastwards travelling water is pushed up against the continental shelf of Western Australia, however this affected by a southwards flowing current of warm, low salinity water that varies in strength with global climatic conditions. Deposits of phosphorites suggest that extensive upwellings occur along the Western Australian coast (Bearman 1989), however the mechanism is poorly understood.

The Leeuwin Current is a compensative, south-flowing mass of warm (24 °C), tropical, low-density, nutrient-poor water that tracks along the 100 fathom line or edge of the continental shelf (Cresswell 1990, Cresswell and Griffin 2000). The current was named after a Dutch vessel of that name (meaning Lioness) which explored the coast in 1622 and it is the dominant feature along the Western Australian coast. The Leeuwin Current flows most strongly between March and October, but has an influence on oceanographic conditions all year round. Since 1982, thermal imaging of the Western Australian coast has tracked the path and strength of the Leeuwin Current (West Coast Sea Surface Temperatures:

<http://www.aodc.gov.au:8888/EAC/servlet/EAC?cmd=result&data>).

It has been suggested that during years of strong Leeuwin Current, cross shore currents and offshore, anti-clockwise flowing loops and eddies drive local upwellings and provide foraging locations for seabirds (Nic Dunlop 2003 pers.com). During El Niño years, when the Leeuwin Current is weaker and the offshore water is cooler along the Western Australian coast, breeding efforts of the Wedge-tailed Shearwater and other seabirds have been observed to crash (Integrated Shearwater Monitoring Program 2000, 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2006).

The Leeuwin Current is characterised by inter-annual differences in flow rates. These arise as the current ameliorates differences in sea levels between northern and southern regions of Australia that arise through differential heating of the Pacific Ocean (Pearce and Walker 1991, Colls and Whitaker 2001). The strength of the Leeuwin Current is directly related to the Southern Oscillation Index (SOI) (Pearce

and Walker 1991), which reflects differences in sea-surface temperatures (which are proportional to barometric pressures) between the Southern Pacific and the Indo-Australian waters. The SOI is generated by subtracting the barometric pressure measured at Darwin from that measured at Tahiti and gives rise to a continuum of numbers. Prolonged negative differences have been labelled El Niño events, whilst La Niña years are characterised by positive values (Colls and Whitaker 2001). These extreme conditions have marked effects not only on flow rate of the Leeuwin Current, but also influence climate, oceanographic conditions, biodiversity and ecology. For example, the influence of the Leeuwin Current facilitates coral growth at higher latitudes than on other seaboards (Pearce and Walker 1991).

During prolonged periods of strongly negative SOI the Leeuwin Current does not flow and therefore, offshore waters remain cooler and water levels are lower. Conversely, when the SOI values are strongly positive, the Leeuwin Current flows stronger and warm water bathes the coast. When disparate water masses interact, upwellings or other features associated with productivity can result (Brooke 2004). Evidently, the presence or absence of a large, mobile body of warm water has the potential to influence not only climate (Colls and Whitaker 2001) but also oceanographic productivity (Pearce 1997). Given its significance the SOI are made available on-line (i.e. [www.bom.gov.au](http://www.bom.gov.au) or [www.fnmoc.navy.mil/PUBLIC](http://www.fnmoc.navy.mil/PUBLIC)). The SOI experienced during this study are presented in Figure 1.4.

The current flows most strongest in the austral winter and reaches different speeds along its southwards path along the edge of the continental shelf. Near the North-west Shelf it flows with a maximum speed of 0.5 knots. From Exmouth southwards

**Figure 1.4** The Southern Oscillation Index experienced during this study from February 2000 to November 2002.

SOI data have been displayed from 1998 to 2003 and prepared by the Commonwealth Bureau of Meteorology on 3 November 2003,  
(<http://www.bom.gov.au/climate/currents/soi2.shtml>)



the current can be seen as jet-like streams of warm water flowing along the continental shelf edge. The shelf edge is often less than 10 km off shore near Exmouth and the current generally flows south at 0.5 to 1 knot (about  $1 \text{ kmh}^{-1}$ ). The current often meanders offshore to form anti-clockwise flowing loops and eddies, often reaching 200 km west. Thermal imaging can reveal three to four loops travelling slowly southwards at a given time between Exmouth and Cape Leeuwin. The shelf widens off Shark Bay, where the current runs further offshore; it also travels more slowly, at speeds of 0.3 knot, with variability in direction (Pearce and Walker 1991). The Houtman Abrolhos Islands are located near the shelf edge and the current runs past them, at a maximum between February and August of up to 1.5 knots. It flows weakly and variably between September and January. Large anticyclonic eddies, of about 200 km in diameter are common features in this area, often dragging cool ocean water in to the shelf and northwards (Cresswell 1990, Pearce 1997, Cresswell and Griffin 2000). Below 250 m depth there is often a northwards undercurrent of 0.2 - 0.3 knot. The speed of the currents along the mid continental shelf (i.e. at 100 m) tends to be northwards at about 0.2 knot in summer and southwards at double that speed in winter. Further south, the Leeuwin Current regularly bathes areas to the west of Rottnest Island as it follows the shelf, but rarely flows east of it. This inshore area is generally affected by a cold northwards flowing current.

The influence of the Leeuwin Current, south of Shark bay, is generally confined to offshore waters, whilst inshore a northwards flowing, cold water current develops. Consequently, winter sea temperatures at the Abrolhos Islands are often  $8 \text{ }^{\circ}\text{C}$  greater than inshore at Geraldton (Pearce 1997). Furthermore, the switch between the 2000 La Niña to the 2002 El Niño resulted in a steady drop in sea levels by 0.2 m,

measured at Fremantle (Ireland 2005). The current spills around Cape Naturalist and its effect can be felt even in the Great Australian Bight and fisheries along the southern coast. When the current is flowing strongly it affects sea surface temperatures at the other side of the continent in the ocean west of Tasmania.

The fluctuations in local climate and oceanographic conditions caused by this global event affects reproduction of summer breeding seabirds along the Western Australian coast (Dunlop and Wooller 1990, Wooller et al. 1991). During El Niño events, Wedge-tailed Shearwater reproduction crashes, while good foraging conditions appear to drive high breeding participation and success in La Niña years (Integrated Shearwater Monitoring Program 2001, 2003, 2006). The existing long-term studies of seabird reproduction will be used as an index of oceanic productivity during the current study.

#### 1.4.4 Climate and seabird reproduction at the Western Australian coast

In many seabird species, phenomena such as the ENSO have implications for breeding seabirds (Cruz and Cruz 1990, Smithers et al. 2003). This is also true on the Western Australian coast, where the climate and resultant annual weather experienced alter the environment in which seabirds operate. An unfavourable annual climate is known to decrease breeding participation and/or success of seabirds on the Western Australian coast (Wooller et al. 1991, Integrated Shearwater Monitoring Program 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, 2006). The annual climate can influence reproductive efforts by reducing the availability of food, changing its location, impeding travel between the colony and foraging sites, and by increasing the occurrence of catastrophes, such as cyclones.

The broad climatic data presented in Figure 1.4 sets the framework within which the research was conducted. Existing long-term studies of Wedge-tailed Shearwaters on the Western Australian coast show how their breeding participation and success fluctuates in accordance with the SOI. Generally, along the Western Australian coast, years dominated by prolonged negative SOI values are characterised by cold, offshore waters and reduced reproduction of summer-breeding seabirds (Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006) and possibly decreases in food availability and overall productivity. The variability of the SOI is shown and the period during which this research was conducted is highlighted from 2000 to 2002. This theme of favourable years with positive SOI values and less favourable years, with negative SOI values will be maintained throughout the thesis.

Table 1.2 provides an interpretation of the climatic conditions experienced at the different locations when research was conducted and summarises the primary aim of each research period. The Wedge-tailed Shearwater provides a useful index, since its reproduction is elevated during periods of positive SOI at the North-West Shelf (Integrated Shearwater Monitoring Program 2001, 2002, 2003, 2006) (Table 1.3) and at the central Western Australian coast (Table 1.4). The climatic data suggest that the most intensive Wedge-tailed Shearwater monitoring during the present study occurred when SSTs were elevated in the 2000/1 breeding season (Table 1.2). Whilst, other intensive research in 2001/2 was conducted before a negative SOI became established. The supplementary feeding was conducted during the 1999/2000 breeding season, when a transition from strong negative to positive SOI conditions occurred. During such times, tropical cyclones appear to occur more frequently along

**Table 1.2** The climatic conditions experienced at different locations during the study of Wedge-tailed Shearwaters and Little Shearwaters over a three year period.

**Table 1.3** A summary of Wedge-tailed Shearwater reproduction at the North-West Shelf in relation to ENSO events (Integrated Shearwater Monitoring Program 2001, 2002, 2003, 2006). The shaded area indicates the duration of this study. Data were collected by Astron Environmental on behalf of Apache Energy.

Breeding season	ENSO event	Wedge-tailed Shearwater egg laying	Wedge-tailed Shearwater breeding success	Possible reason
1997/98	Strong El Niño	Extremely low	Extremely Low	Cool water only
1998/99	Changing from El Niño	Moderate	Catastrophic	Warm water starting to move down the coast, but also Tropical Cyclone Vance at end of March
1999/2000	La Niña	High	High	Warm water
2000/01	La Niña	High	High	Warm water
2001/02	Changing, but more La Niña	High	Moderate	Transition from warm to cool waters
2002/03	El Niño	Low	Low	Cool water
2003/04	Changing from El Niño	Moderate	Catastrophic	Warm water starting to move down the coast but also Tropical Cyclone Monte at the end of March

**Table 1.4** The percentage of active burrows used for breeding on Lancelin Island and Rottnest Island, in different breeding seasons. Data were collected by Astron Environmental on behalf of Apache Energy.

Breeding season	Percentage of active burrows		
	West side	Lancelin Island South side	Rottnest Island Cape Vlamingh
2000/2001	36	32	29
2001/2002	29	29	26
2002/2003	16	11	25
2003/2004	18	10	
2004/2005	5		
Number of burrows surveyed	100	50	100

the Western Australian coast (Dr Nic Dunlop, 2003 pers. comm.). At higher latitudes, these result in heat trough and prolonged periods of low wind conditions. The impact of a long period of low wind speed upon nestling feeding will be explored in Chapter 6.

Unlike other species studied along the Western Australian coast, the Little Shearwater breeds in winter, when the Leeuwin Current flows most strongly. In winter 2000, the SOI was strongly positive (La Niña year), suggesting that a strong Leeuwin Current transported warm, low-density water to higher latitudes. As a result, warm water immersed the central Western Australian coast and vast sections of offshore waters, as demonstrated by west coast sea surface temperatures from 19 September until approximately 17 October 2000. Large eddies were evident on these images and it is possible that food chains develop at such thermoclines. This warm water intrusion overlapped much of the Little Shearwater parental provisioning period in 2000. Since Little Shearwaters are small and feed their nestlings daily, it is highly likely that they forage at locations influenced by the Leeuwin Current. This will be explored using opportunistic observations at sea and existing observations at sea.

In 2001, the SOI was highly variable, but mostly negative; as a result, the Leeuwin current was weaker. West coast sea surface thermal imaging showed that coastal and offshore waters were cooler, with only a skinny finger of warm water extending to the central coast of Western Australia. In 2002, the SOI was mostly negative (El Niño year) and the current was even weaker, with warm water persisting only at higher latitudes, near Shark Bay. In 2001 and 2002, the temperature profile remained fairly constant over the same period owing to poor current flow. During this period the tuna

industry operating out of Geraldton experienced poor catches (Craig Culliver 2002, pers. comm), suggesting an absence of the smaller fish, which attract and support larger pelagic fish. Also the settlement of Western Rock Lobster puerulus was reduced in that year (Dr Nic Dunlop, 2002 pers comm.). Along the Western Australian coast, a relationship between SOI and Western Rock Lobster pueruli settlement has been established, which influences the catch with a four year time lag (Pearce and Phillips 1988, Kailola et al. 1993). Long-term records from Western Australian commercial fishing industries, and records of seabird reproduction, increasingly point towards an overall crash in offshore productivity in association with uniform and/or cold SSTs.

From a seabird perspective, the conditions on the Western Australian coast appear to be neither stable nor predictable between years nor within a year. The differences in environmental conditions experienced (Figure 1.4) meant that the study was conducted during a “favourable year in 2000” with prevailing La Niña conditions, which facilitate seabird reproduction. This was followed by a “transition year in 2001” and a “less favourable year in 2002” dominated by El Niño conditions, which have been associated with poor seabird reproduction at the Western Australian coast.

## **1.5 Attributes of the two shearwater species**

### **1.5.1 Flight and foraging at sea**

Finding ephemeral, highly dispersed foraging sites in a vast ocean can be difficult, especially on the Western Australian coast where no stable zones of upwelling are thought to exist. Some tube-nosed birds are thought to locate prey using olfactory cues, as the ocean resembles an olfactory landscape (Nevitt 1999, 2000). Olfactory

cues are most effective in cool climates (Prince and Morgan 1987, Nevitt 1999, 2000). Sight is also used to locate prey and often the movements of other predators are monitored, including conspecifics (Prince and Morgan 1987, Warham 1996). The energetics involved in searching large expanses of ocean indicate that an interplay may exist between the small scale variables generated large scale weather systems, that facilitate travel in the short-term. Consequently, the climate experienced may influence the foraging efficiency of different species in accordance to the limitations of their functional morphology.

The two congeneric species of shearwater studied, the Wedge-tailed Shearwater and Little Shearwater, are disparate species, thought to be suited for tropical and temperate conditions respectively (Section 1.5.2). Their breeding distributions overlap on offshore islands along the Western Australian coast in a subtropical climate. However, the Little Shearwater breeds during the austral winter when a more temperate climate is experienced and the Leeuwin Current achieves maximal flow rates (Cresswell 1990, Cresswell and Griffin 2000). In contrast, the Wedge-tailed Shearwater breeds in the austral summer, when conditions are warm and dry and the Leeuwin Current weakens, leaving behind cold or warm offshore waters in accordance with its strength during the previous winter (Cresswell 1990, Pearce and Walker 1991, Pearce 1997, Cresswell and Griffin 2000). The difference in morphology may reflect difference in their ability to adjust to proximal weather conditions and this will be investigated in this study.

Most Procellariiformes engage in dynamic soaring, which provides an energetically efficient way of travelling long distances (Warham 1990). The Little Shearwater is



the lightest species in the genus *Puffinus* and has skinny wings with a small area, resulting in high aspect ratio and wing loading. Birds with a high wing loading need to maintain higher flight speeds as they are more likely to stall (Warham 1996). Since wing loading is a function of weight, it can be highly variable for each individual depending on the phase of the life cycle. Payloads carried are costly as they may decrease the energy efficiency of flight. The weight problem is further compounded when winds are too low to allow shearwaters to use dynamic soaring as an efficient means of locomotion.

Generally, flapping flight is more energetically expensive than dynamic soaring (Warham 1990). The Little Shearwater is often encountered in flapping flight, travelling close to the water surface in the friction layer and may only use dynamic soaring in stronger winds, perhaps due to its relatively high wing loading. The Little Shearwater is unusual among shearwaters, in being able to fly close to the velocity for maximum range under flapping flight. A flight speed of about  $14 \text{ ms}^{-1}$  would be associated with increased power requirements, while flight at  $10 \text{ ms}^{-1}$  would be economical (Alerstam *et al.* 1993 cited in Warham, 1996). In contrast, the Wedge-tailed Shearwater, with its lower wing loading, is able to use dynamic soaring under less windy conditions and is rarely seen flapping in flight, although it may revert to flap-gliding in times of low winds. Effectively, this study deals with two species that differ in their wing designs and hence, flight potential geared to survive in the disparate weather patterns expected to prevail in summer and winter. Consequently, parental provisioning in both species may be affected by weather patterns, and this was investigated during this study.

Weather patterns may not only affect the ability of shearwaters to engage in low energy locomotion, but it may also affect the direction of travel and time taken to cover distances. Procellariiformes rarely fly with tailwinds, their flight path generally being at right angles across the wind or at an angle to the head wind. However, species with low wing loading travel into headwinds more often and are more likely to fly with tailwinds, whilst Manx-type shearwaters were rarely seen to do so (Spear and Ainley 1997a). Little Shearwaters are grouped among glide flappers, together with other Manx-type shearwaters and diving petrels. Whilst, Wedge-tailed Shearwaters have been classified as flap gliders among other surface-feeding shearwaters, including the Fleshy-footed Shearwater (Spear and Ainley 1997b). Furthermore, flight speeds generally increase with increasing headwinds (Spear and Ainley 1997b), indicating that birds may be able to travel more rapidly during certain weather conditions. Generally, wind speeds increase as pressure differences between adjacent weather systems increase. Consequently, shearwaters activity at the colony will be measured and tested in regards to different weather variables generated by the passage of different weather systems.

The slight differences in the morphological features which affect flight potential evident between the different shearwater species may also affect dive potential. Wing loading is thought to be inversely proportional to buoyancy and can be seen as indicative of dive potential. The Wedge-tailed Shearwater has very broad wings and together with Buller's Shearwater, has an unusually low wing loading for its mass (Warham 1996). This, combined with a long tail, lends the Wedge-tailed Shearwater great aerial dexterity. Consequently, Wedge-tailed Shearwaters are thought to be very buoyant birds that have difficulty diving to great depth (Brown et al. 1978). Indeed,

Wedge-tailed Shearwaters have been observed surface seizing and contact dipping, but are rarely seen at greater depth (Marchant and Higgins 1990). However, a study using maximum depth gauges suggested that Wedge-tailed shearwaters were able to attain an average maximal dive depth of 14 m and a maximum depth of 66 m (Burger 2001), despite being a more buoyant bird in flight (Brown et al. 1978). The narrow wings of the Little Shearwater are indicative of an even greater dive potential and maximum depth gauges will be utilised to measure dive depths in this study.

Feathers in optimal condition are necessary for both efficient flight and underwater propulsion (Warham 1996). The plumage of Procellariiformes is very oily, which allows total submergence without water logging (Warham 1996). Some species of shearwaters are highly skilled at underwater locomotion and engage in pursuit diving, during which their half-folded wings are used for propulsion to apprehend prey underwater (Warham 1990). Little Shearwaters are known to pursuit dive from both the surface and the air in the Western Atlantic and are morphologically suited for diving (Brown et al. 1978), although surface-seizing and surface diving also occur (Marchant and Higgins 1990). Similar behaviours have been observed for the Wedge-tailed Shearwater (Marchant and Higgins 1990). Dive depths are currently not available for the Little Shearwater, but the similarly sized Audubon's Shearwater reached an average maximal depth of 15 m and a maximum depth of 35 m (Burger 2001).

### 1.5.2 The Little Shearwater

The Little Shearwater weighs 142-201 g, and is 24-31 cm long with a wingspan of 55-60 cm (29/62, these values representing body length/wingspan in cm are sourced from

Harrison, 1985 when available). The smallest species within the genus *Puffinus*, the Little Shearwater is similar in size to Audubon's Shearwater (30/69, 150-230 g). Species within the Audubon's and Little Shearwater complex are closely related (Austin et al. 2004) and are all winter breeders, with similar egg sizes, incubation and fledging periods. However, unlike the Little Shearwater, colonies of Audubon's Shearwater (and the Christmas Island Shearwater *Puffinus nativitatis* 36/76) arrive at the colony during the day to feed nestlings and lay eggs throughout the year, although individual pairs do not relay (Harris 1969b).

The Little Shearwater is part of a congeneric complex of birds that are recognised by their counter-shading (being essentially white below and grey above). These include Audubon's Shearwater, the slightly larger Fluttering Shearwater *Puffinus gavia* (33/76), Manx Shearwater *Puffinus puffinus* (34/82), Hutton's Shearwater *Puffinus huttoni* (38/90) and the much larger Buller's Shearwater *Puffinus bulleri* (46/97) (Slater et al. 1986, Marchant and Higgins 1990, Johnstone and Storr 1998). Among these, the Little Shearwater is the only species with blue legs. However, at sea, the Little Shearwater can be mistaken for smaller species in this complex. Other shearwaters, such as Cory's Shearwater (49/111) and the Streaked Shearwater *Calonectris leucomelas* (length: 46-51 cm) are similar in colour, but are much larger and belong to a different genus.

The Little Shearwater is a polytypic species, whose taxonomy needs revision (Austin et al. 2004). Currently, accepted taxonomy recognises the existence of a *Puffinus assimilis tunneyi* on islands off the Western Australian shore (Marchant and Higgins 1990). Another six subspecies breed on islands at different locations around the globe, with only one found in the northern hemisphere, in the North Atlantic, off the

north-west African coast (Warham 1990). Several subspecies of the Little Shearwater have been studied, for instance the larger and heavier *P.a. haurakiensis* on islands off the north-eastern coast of the North Island in New Zealand (Booth et al. 2000, Booth et al. 2000b) and *P.a. assimilis* on Lord Howe Island off the East Australian coast (Bester 2003). *P.a. baroli* was studied in the North Atlantic on Selvagem Grande (Hamer 1994) at approximately 30° N and 16° W and is more closely related to Audubon's Shearwater than the other currently recognised subspecies of the Little Shearwater (Austin et al. 2004). The Western Australian subspecies was studied on Eclipse Island, near Albany, off the south-western coast of Western Australia (Glauert 1946, Warham 1990). Other subspecies breed on small islands in the southern Pacific, *P.a. kermadecensis* on the Kermadec Islands and *P.a. elegans* on the Chatham and Antipodes Islands, while, *P.a. myrtae* breeds in the Austral Group and southern central Pacific Ocean (Glauert 1946, Warham 1990). *P.a. tunneyi* is the smallest race of the species (Marchant and Higgins 1990).

Current phylogenetic investigation based on mitochondrial DNA cytochrome-b gene suggests that the northern hemisphere, *P.a. baroli* is more closely related to Audubon's shearwater and differs from the southern hemisphere and subtropical-subantarctic clade containing the Australasian and Southern Ocean *assimilis* taxa. This is indicative of the existence of a physical barrier between the southern and northern hemisphere. Within the Australasian and Southern Ocean clade, speciation appears to have occurred on individual islands or island archipelagos, with *P.a. myrtae* the least similar of the other five *P. assimilis* and possibly more closely related to Newell's Shearwater *P. newelli* (Austin et al. 2004). This suggests that

research conducted in the Northern Hemisphere, focused on *P.a. baroli* (Hamer 1994), may not be as relevant to *P.a. tunneyi* as research focused on *P.a. haurakiensis* in New Zealand (Booth et al. 2000, Booth et al. 2000b). Furthermore, the New Zealand subspecies exist in the same hemisphere, although breeding at a higher latitude.

Little Shearwaters breed at mid to high latitudes in both hemispheres, although most breeding activity occurs in the southern hemisphere. Little Shearwaters frequent subantarctic, subtropical and occasionally tropical waters (Marchant and Higgins 1990), but it may be assumed that adults forage in cool waters. During the winter months, the warm Leeuwin Current streams southwards, west of the Houtman Abrolhos Islands, while, along the coast, an opposing current of cooler water moves northwards. Initially, it was predicted that the Little Shearwater would utilise these inshore, cool waters for foraging. Observations on fishing vessels and existing information were used to examine this proposition (Chapter 8). Furthermore, a cold-water forager may be expected to thrive in years of low Leeuwin Current flow, when offshore waters remain cooler, unlike tropical, summer breeding birds that have been extensively monitored along the Western Australian coast.

Glauert (1949) published data collected by two lighthouse keepers on Eclipse Island off the south-west coast of Western Australia near Albany, which focused on *P.a. tunneyi*. To date, this summation of the research conducted mainly by A.V. Newman and instigated by A. Blythe provides the most detailed account of the subspecies breeding in Australian waters. Little Shearwaters arrive at the colony at night. Eggs are laid in June to July, which hatch in late August to September. Nestlings fledge in

late October to mid November (Table 1.1b). An incubation period of 52-58 days (n = 4) was recorded and adults were thought to relieve partners every two days. A nestling period of 70-75 days was observed, with the nestling fed every second night by both parents for the first fortnight and then once or twice every five nights thereafter. A fasting period of 8-10 days was observed before fledging (Glauert 1946).

### 1.5.3 The Wedge-tailed Shearwater

The Wedge-tailed Shearwater is much larger than the Little Shearwater, weighing 300-570 g and being 38-46 cm long, with a wingspan of 97-105 cm (43/101).

Predominantly, it is a brown bird with often pink or grey legs, although a small number of light phase birds appear to breed in the Shark Bay region and can be seen in waters off Kalbarri (Serventy 1972, Wooller et al. 2005), Hawaii (pers. com Dyer 2006) and occasionally at the Houtman Abrolhos Islands (pers. observation 2003).

Wedge-tailed Shearwaters are less placid when handled than Little Shearwaters and bite harder. Birds of similar colouration that breed along the Australian coast include the Short-tailed Shearwater (42/98 length: 40-45 cm) and Fleshy-footed Shearwater (43/103) (Slater et al. 1986, Marchant and Higgins 1990, Johnstone and Storr 1998).

Both are heavier birds than the Wedge-tailed Shearwater, but look and behave similarly at sea. Fleshy-footed Shearwaters often forage in large numbers in offshore waters off the Geraldton coast from February to October (pers. observation). The other shearwater in Australasia, which breeds off the south-eastern coast of Australia, is the Sooty Shearwater *Puffinus griseus* (44/99), which is sooty-brown and has white underwings that result in characteristic white flashes when banking (Harrison 1985).

The Wedge-tailed Shearwater is a summer breeder, which arrives on Rottnest Island in August to September to prospect burrows and find mates. A pre-laying exodus occurs in November and laying begins in late November (Garkaklis et al. 1998). Nestlings hatch in mid January and young fledge from mid-April to early May near Perth (Garkaklis et al. 1998), (Table 1.1c). The timing of breeding events along the Australian coast appears to be influenced by latitude. For example, key events in the Wedge-tailed Shearwater breeding cycle occur earlier at lower latitudes such as the North West Shelf, than at higher latitudes, such as Rottnest Island. Incubation periods are similar in duration to the Little Shearwater at around 52-54 days (Marchant and Higgins 1990), but nestling periods (109 days) are longer (Serventy et al. 1971).

#### 1.5.4 Breeding distribution of both species in Western Australia

The distributions of the Wedge-tailed Shearwater and Little Shearwater overlap (Harrison 1985, Brooke 2004). The Little Shearwater is at the northernmost limit of its range at the Houtman Abrolhos Islands where large colonies (estimated at 10 000 birds) of the species occur on Leos Island and West Wallabi Island. Colonies of less than 100 pairs breed on the small, limestone islands further south along the west coast from Dongara to Perth, with larger colonies on islands off the south coast of Western Australia, from Albany to Esperance (Burbidge and Fuller 1993). In contrast, the Wedge-tailed Shearwater can be found in subtropical regions on either side of the equator, predominantly in the Pacific and Indian Oceans (Harrison 1985). The largest breeding colony on the Western Australian coast is located on West Wallabi Island (Fuller *et al.* 1994). The furthest south that the Wedge-tailed Shearwater breeds in Western Australia is on Carnac and Rottnest Islands, near Perth (Burbidge and Fuller 1993).



### 1.5.5 Migration

For seabirds, the annual cycle can be divided into reproductive events and a period during which feathers are replaced and body condition is gathered for the next breeding attempt. Some species, such as the Short-tailed Shearwater or the Sooty Shearwater, migrate to other areas when not breeding and are dependent upon resources seasonally available at higher latitudes. The predictable and high availability of resources, outweighs the constraints imposed by their seasonality, as demonstrated by the increase in seabird density and abundance at higher latitudes (Brooke 2004). After conditions deteriorate, the large populations must migrate long distances in order to maintain future reproductive potential.

Transequatorial migrants, such as the Sooty Shearwater, Short-tailed Shearwater and Manx Shearwater have been studied intensively and have contributed greatly towards theories of nestling obesity. Neither, Wedge-tailed Shearwaters nor the Little Shearwaters are thought to operate under such temporal constraints. Wedge-tailed Shearwaters appear to disperse into the Indian Ocean, but can be seen along the Western Australian coast during the non-breeding season at least at more tropical locations. Some individuals may ride weather systems to far locations, but as a whole the populations do not appear to migrate. The Little Shearwater is thought to be even more sedentary and visits its breeding colony nearly all year round, except between the end of fledging in November until January (Glauert 1946). Consequently, Little Shearwater nestlings were not expected to be deserted by their parents before fledging.

## 2 Chapter 2: General Methods

### 2.1 Introduction

Two congeneric species of *Puffinus* shearwaters were studied at different times of the year and at different locations along the Western Australian coast. The Little Shearwater is a winter breeder, which lays a single egg in July, that hatches in late August to late September and all nestlings fledge by late November. The Wedge-tailed Shearwater is a summer breeder, which lays a single egg in November the nestling hatches in January and fledges by late April or early May. The temporal difference in their breeding seasons made it possible to study parental provisioning in both species, although focusing primarily on the breeding biology of the Little Shearwater. The use of congeneric species meant that differences between them could be related to environmental factors, rather than phylogenetic constraints (Harvey and Pagel 1991).

The Little Shearwater was an important species to study as it represents an additional case in the suite of shearwaters studied, which inhabit the Indian and Southern Oceans. Only limited data were available for the Little Shearwater breeding off the Western Australian coast, which suggested that Little Shearwaters feed their nestling near daily (Glauert 1946, Warham 1955). In species that feed nestlings near daily, obesity would not be expected to serve as a buffer against irregular arrival by adults. Similarly, the Wedge-tailed Shearwater appears to feed their nestling near daily. The Wedge-tailed Shearwater served as a good comparison with some existing data available on the species breeding along the Western Australian coast (Garkaklis et al.

1998, Nicholson 2002) especially in terms of long term breeding participation and success in response to variable oceanographic conditions (Wooller et al. 1991, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2003). Although, the Wedge-tailed Shearwater is a more tropical species than the Little Shearwater their distribution overlap on the Western Australian coast and it serves to anchor the short term research to existing long-term study focused on the availability of oceanographic resource along the Western Australian coast. The objectives of the research were introduced in Chapter 1 (section 1.2). Table 2.1 provides a summary of general objectives and potential techniques employed to document seabird behaviour.

## **2.2 Methodology**

The main focus of the fieldwork involved visiting breeding sites and handling seabirds over a time frame February 2000 to November 2003. This focused on parental provisioning and development. Additional research was conducted as further questions arose about the adults conduct at sea, which was the driving force of the observations at the breeding colony. This included the stable isotope analysis and maximal depth gauges. Limited funds combined with remote nature of the study site (90 km from Geraldton) which is not inhabited during the nestling period of the Little Shearwater resulted in reliance upon lifts from the fishing community and charter boat industry. Whilst, accommodation had to be provided by the Department of Fisheries WA, as fishing camps are only to be used for purposes pertaining to fishing activities. Although research aims were planned, implementation always maintained an opportunistic element.

**Table 2.1** The objectives of the study and field techniques utilised.

Focus	Objectives	Field technique
Little Shearwater incubation behaviour	Adult little Shearwater weights during incubation and durations of incubation shifts	Daily visits using burrowscope Subset of adults weighed and handled
Hatching patterns	Should be asynchronous as resources do not predicably shut down, as seasonally occurs at high latitudes	Daily visits using burrowscope
Guard behaviour	Do Little Shearwaters attend to nestling after hatching?	Daily visits using burrowscope
Provisioning	Is adult presence at breeding site influenced by weather?	Daily weighings, nocturnal activity surveys
Provisioning of food	Define meal size and rate of food delivery (frequent weighing and daily weighing)	Frequent weighing (short term only)
Provisioning of food	Patterns of food delivery over time	Daily weighing of nestlings twice daily
Provisioning of food	Examine shearwater provisioning under variable conditions within a year and between different years	Daily weighing of nestlings twice daily Frequent weighing
Obesity	Should not overfeed: Regular visits/feedback. No migration	Daily weighing of nestlings twice daily
Obesity	May need a fat buffer in an unstable environment in terms of oceanographic conditions and weather patterns	Daily weighing of nestlings twice daily Respirometry
Mechanism of parental provisioning – Little Shearwater	Little Shearwater were expected to forage near colony as feed nestling regularly	Observations at sea, departure and arrival behaviour, direct and indirect measures of adult attendance
Mechanism of parental provisioning	Supplement feeding to see if adults adjust provisioning to fed nestlings (able to respond to nestling condition)	Supplement feeding– Wedge-tailed Shearwater
Mechanism of parental provisioning	Changes in oceanographic conditions/climate: Examine more subtle mechanism of why seabirds struggles to supplement knowledge on decreased breeding participation or success	Directly- monitoring adults during frequent weighing Indirectly - by daily weighing of nestlings and nocturnal activity pattern of adults
Mechanism of parental provisioning	Little Shearwater adult weights during nestling feeding	Directly – monitor adults frequent weighing
Mechanism of parental provisioning	Co-ordinated parental care does it change with time?	Directly – monitor adults frequent weighing

**Table 2.1** – Continued. Objectives of the study and field techniques utilised.

Focus	Objectives	Field technique
Desertion	Should not desert nestling, no migration.	Daily weighing
Pre-fledging weight loss	Examine changes in the basal metabolic rate in Wedge-tailed shearwater nestlings using respirometry	Daily weighing
Nestling growth	Measure growth of nestlings	Weekly morphometrics
Nestling growth	Monitor feather growth	Weekly morphometrics
Little Shearwater foraging location	Forage near colony in cooler, inshore waters	Observations at sea, existing observations
Little Shearwater dive depths	Has high wing loading, therefore less buoyant bird than the Wedge-tailed shearwater and likely to engage in deep dives. Leg morphology unknown, investigate this and relate to dive potential.	Maximum depth gauges Measure leg morphology
Little Shearwater dive depths	Dive depth increases with time at sea Focus on different phases of provisioning	Maximum depth gauges and patterns of retrieval give direct indication of adult attendance
Little Shearwater travel and weather	May utilise weather systems for travel	Daily and frequent weighing: adult patterns Nocturnal surveys
Little Shearwater	Investigate presence at colony at night	Adult presence during frequent weighing
Wedge-tailed Shearwater	Investigate presence at colony at night	Adult presence during frequent weighing
Wedge-tailed Shearwater travel and weather	May utilise weather systems for travel. Broad wings, able to survive low wind situations	Daily weighing
Evaluation of stable isotope analysis	Able to detect differences between species, within species at different location and times (seasonal changes in diet)? Use to detect competition of predators with fishing industry?	Stable isotope analysis

Observations at sea were always opportunistic, whilst obtaining lifts to the study site or working on fishing vessels to supplement my income from 2001 to 2004 (Table 2.2). Consequently, observations at sea represent extended period of time spend working at sea, watching the ocean and seabirds at sites targeted by the fishing industry or charter boat industry. These observations were supplement with input from fishermen skilled at identifying seabirds at sea, David Mitchell and Craig Culliver; and unpublished observations generously supplied by Dr Dunlop and Dr Surman.

This chapter introduces most methods utilised. Evidently, every year burrows were located and birds banded to facilitate reliable identification. Other methodology is provided in relevant chapter, as for example nocturnal activity surveys (Chapter 3), analysis of adult attendance during frequent weighing (Chapter 4), correlations between adult behaviour and weather patterns using cross correlation frequency analysis (Chapters 3 and 4), supplementary feeding (Chapter 6) and respirometry (Chapter 6).

The arrival patterns of adults at the colony may be difficult or time consuming measure. Consequently a range of indirect methods were utilised, which were able to be maintained for a longer period of time. Generally, the use of barricades erected at the entrance of burrow was of limited use to monitor the movement of shearwaters was not robust, as conspecifics, Bridled Terns and other species appeared to confound results. Indirect methods to gain an index of adult attendance were explored, included nestling weight gain recorded during daily weighing and nocturnal activity surveys

**Table 2.2-** Field work conducted which contributed to the content of this thesis.

Year	Wedge-tailed Shearwater	Little Shearwater	Location
2000	Intermittent daily weighing and morphometrics Supplementary feeding		Pelseart Island  Pelseart Island Beacon Island Beacon Island Beacon Island Inshore: Geraldton to Islands
2001	Hatching attempt- cut short: injury Daily weighing Morphometrics Frequent weighing		Lancelin Island Lancelin Island Lancelin Island Beacon Island Beacon Island
		Incubation/Hatching Daily weighing Stay at site cut short: limited access to camp Morphometrics ongoing weekly visits Search at sea: travel	Beacon Island  Inshore: Geraldton to Islands
2002	Hatching Daily weighing focus fledging Limited morphometrics		Rottnest Island Rottnest Island  Rottnest Island
		Search at sea: working on cray boats: February	Big Bank area, north of Abrolhos Islands to Kalbarri
	Frequent weighing Respirometry Stable isotopes Stable isotopes Stable isotopes		Rottnest Island Rottnest Island Rottnest Lancelin North-West shelf
		Search at sea on fishing vessels: May –June Daily weighing Morphometrics Frequent weighing Maximum depth gauges Stable isotope Search at sea: travel	North and west of Abrolhos Islands Beacon Island Beacon Island Beacon Island Beacon Island Beacon Island Inshore: Geraldton to Islands
2003	Search at sea (working on cray boat)		Lancelin area January-February
		Search at sea (working on cray boat)	Inshore areas near Geraldton to Islands
2004		Search at sea (working on wet liner)	Geraldton to Islands, north and west of Islands

### 2.2.1 Locating burrows and monitoring hatching

Burrow occupancy was checked using a burrowscope (Dyer and Hill 1991, Nicholson 2002, Dyer 2003) when one was available and functional. A burrowscope generally consists of an image recorder fitted with an infra-red light and a display unit. The camera lens of a security camera, mounted on a pliable extension was guided into a burrow, while the display unit remained on the outside, where a black and white image could be seen. The use of a burrowscope minimised disturbance to the birds and was used extensively during the incubation period to avoid damage to the egg. Burrows were also checked by hand, when a functional burrowscope was not available. However, this limited monitoring to short burrows where the nest cavity could be reached with minimal modifications to the burrow. On Rottnest Island, the use of a burrowscope was necessary for the Wedge-tailed Shearwater, since most burrows were long. Similarly, on Beacon Island, an inability to monitor long burrows during the hatching time resulted when the burrowscope became inoperative, almost halving the sample size.

Once nestlings had hatched, and the guard period was over, burrows were monitored by hand. The short, accessible burrows were supplemented with some long burrows to reduce potential bias. Suitable long burrows were modified to allow extraction of the nestling (approximately 40 % of sample size). To minimise disturbance, long burrows in sandy areas were chosen away from dense vegetation and a second entrance was dug, often in the roof of the tunnel to access the nestling. When not used, this hole was covered with vegetation or coral shingles. Burrow modification occurred after the adult was no longer present during the day to ensure the duration of the guard periods was not influenced by our behaviour. Although, some data were



gathered during the incubation period, ultimately one aimed to minimise risk and to ensure that enough nestlings were available to complete the food delivery facets of the study.

### 2.2.2 Incubation shifts of the Little Shearwater

Accessible burrows were visited daily to check egg status. The adult was identified and weighed ( $\pm 1$  g) using a digital scale. Adults were marked using waterproof marker, which washed off while at sea, making it easy to identify adults returning from sea. If incubating birds did not face the right way to see the mark, the burrow was revisited later in the day. Once nestlings had hatched, adults were no longer removed, in order to monitor the length of the guard period and to ensure that the nestling was not disadvantaged by our activities. More details are provided in Chapter 3.

### 2.2.3 Banding

Adults and nestlings were banded, once tarsi were completely grown, according to the guidelines of the Australian Bird and Bat Banding Scheme. Wedge-tailed Shearwaters were banded using conventional ovalised bands (size: 16) and long-nosed pliers, while size 06, round bands had to be ovalised for the Little Shearwaters in accordance with the Australian Bird and Bat Banding Scheme (David Dryan 2000, pers. com.). Pliers were modified, by cutting an oval shape into the cutting section of the pliers. This allowed consistent ovalisation of the round bands.

### 2.2.4 Morphometrics

Nestlings were measured at approximately seven-day intervals, when possible.

Vernier callipers ( $\pm 0.1$  mm) were used to measure head-beak, culmen length, beak

depth at gonys, tarsus length, plumage components and a butt-ended wing ruler (0.3 m long,  $\pm 1$  mm) was used once the tail and wing measurements were larger. The tarsus, measured the length of the tarsometatarsus from the distal joint to the exposed edge of the tarsometatarsus. It did not include the distal end of the tarsus or the tarso-tarsometatarsal joint, as is often the practice (Powell 2000). The tarsometatarsal ratios were obtained for each species using Little Shearwater adults and Wedge-tailed Shearwater nestlings prior to fledging, when their legs should have reached adult size. The tarsometatarsus was measured twice at the midpoint, once to gauge medial-lateral flattening of the leg and a second time to measure its anterior-posterior width. The ratio was derived from dividing this maximal width from the latter measurement.

Plumage was measured as the length of the feather or length of feather sheath if the feathers had not hardened and uncovered. The fifth covert was measured, which erupted before the primaries began to grow. In addition, the dorsal down was measured between the shoulder blades. A feather was chosen within the second line depicted by protoptile directly behind the wings and on top of the body.

Approximately the same feather, or neighbouring feather within the same line, was monitored throughout its growth phases on all nestlings. Similarly, the tail feathers were measured by picking the central feather. Initially the down was measured and later the developing contour feather. Once the feather was longer, a butt-ended ruler was inserted under the feather until it touched the base of the top, central feather.

#### 2.2.5 Daily weighing

After the guard period had ended, usually after about a week, nestlings were weighed ( $\pm 1$  g) twice daily using a digital scale. The accuracy of the scales was tested

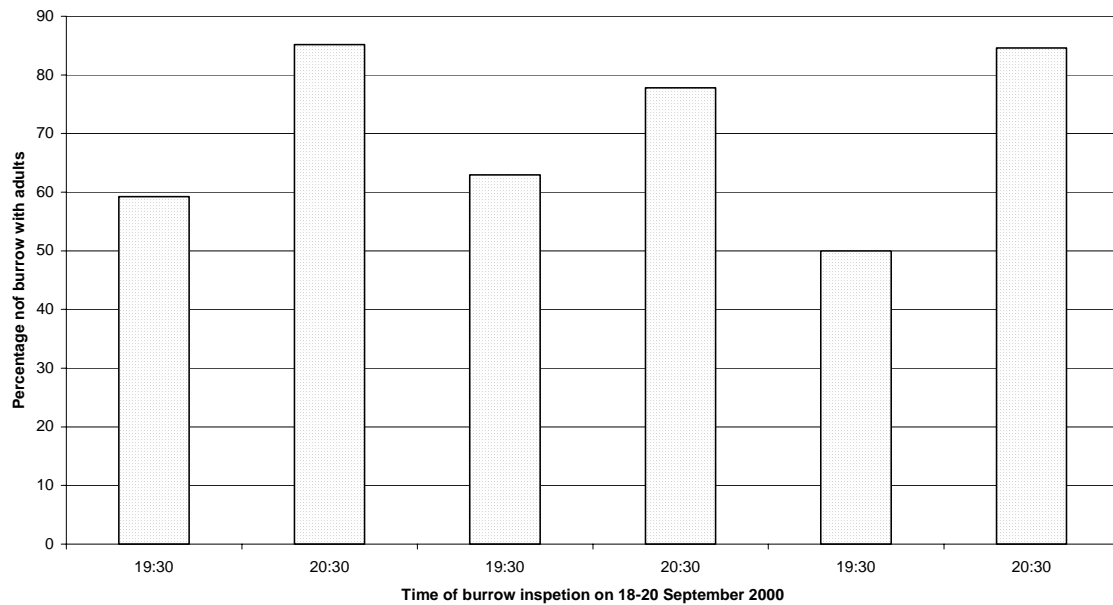
intermittently using a known weight. Early in ontogeny, the nestlings would sit unrestrained on the scale; later, once feathered, they had to be wrapped in a cotton bag to remain settled. When resident on Beacon Island, weighing occurred at 05:30 h and 17:30 h, while on Lancelin Island and Rottnest Island weighing occurred at 09:30 h and 17:30 h. The later times were related to the time needed to cycle to the beach, swim to the mooring and drive the dinghy to the Lancelin Island in 2001. On Rottnest Island, a car was intermittently available to travel to the field site approximately 6 km away; however, often a bicycle was used for travel, in keeping with Rottnest Island tradition and to save research funds. Daily weight changes in nestlings were utilised as an indirect method of monitoring the level of parental care provided by adults over longer periods of time (Chapter 4 and 6).

#### 2.2.6 Frequent weighing

Frequent weighing involved weighing nestlings at regular intervals during a complete night to determine the actual meal sizes delivered by adults. The arrival pattern of adult Little Shearwaters at Beacon Island was used to determine the temporal intervals used during frequent weighing, which was later also applied to the Wedge-tailed Shearwater to allow comparison between the two species. In all, 29 Little Shearwater burrows without adults present during the day were visited after sunset at 19:30 h and 20:30 h when nestlings were present. By 20:30 h adults were present at around 80 % of burrows (Figure 2.1). To allow for feeding to have occurred, 21:30 h was chosen as a suitable time for weighing. This time was four hours after the afternoon weighing. Thereafter, nestlings were weighed at 4 h intervals until dawn (namely at 21:30 h, 01:30 h, 05:30 h). For the Wedge-tailed Shearwater, another weighing at 09:30 h was completed to correlate frequent weighing data with the twice daily weighing.

The four-hour intervals between successive weighing were thought to have minimised any impact upon the nestlings and adults, to ensure feeding occurred. Little Shearwaters that were often present throughout the nights. In contrast, Wedge-tailed Shearwaters often fed their nestlings, then disappeared or sat outside the burrow, only to disappear once the observer appeared. The persistent presence of adult Little Shearwaters at night resulted in many adults being banded, so that their band numbers and body weights could also be monitored at night. Despite this frequent handling, adult Little Shearwaters remained present throughout the night, unlike Wedge-tailed Shearwaters. The study was therefore able to comment upon the foraging strategy employed by the Little Shearwater and explore weight changes during provisioning, whereas this was not feasible for Wedge-tailed Shearwaters.

Frequent weighing was used to determine meal sizes for the Little Shearwater on Beacon Island in the period from late September to early October 2000 (six nights), in early October 2001 (3 nights) and in October 2002 (3 nights). For Wedge-tailed Shearwaters, meal size was determined on Lancelin Island in late March 2001 (five nights) and on Rottneest Island in mid April 2002 (three nights). Frequent weighing was utilised to determine the relationship between daily weight changes and meal sizes delivered. Consequently, more robust data would be created with a larger number of meals delivered. Given that adult attendance at the colony was observed to fluctuate with time, frequent weighing was timed to target weather conditions that promised large adult attendance at the colony. This maximised return for effort, during short term intensive research. Short- term research is always biased to



**Figure 2.1** 27 burrows were monitored at 19:00 h and 20:00 h on 18, 19 and 20 September 2000 to determine the nocturnal arrival of the adult Little Shearwaters at burrows without an adult present during the day. This was used to determine a suitable time to initiate frequent weighing.

prevailing weather conditions and also exhausting to conduct. For example, on Rottneest Island, frequent weighing was started after several days of calm, north-easterlies during which nestlings had not been fed. Subsequently, a high proportion of nestlings were fed during the passage of the next front, leading to a relatively short period of night work. This implies that feeding frequency, determined over short periods of frequent weighing, may not necessarily be representative of actual feeding rates. Further endeavours were made to document the changes in adult attendance over time, using indirect and less exhausting methods. For example daily weighing

data were used to approximate adult attendance and nocturnal activity surveys were conducted and analysed for correlations with prevailing weather conditions.

### 2.2.7 Analysis of data for frequent weighing of nestlings

The weight increase recorded during a 4 h sampling interval is not the actual amount of food ingested during the interval, because nestlings lose weight through respiration, evaporation and defecation. The aim of the statistical analysis was to find a regression equation that would correct for inherent weight loss and determine corrected meal sizes delivered overnight. The regression equation was also used to estimate the amount of food accepted by the nestling overnight, based on daily weights. Data analysis was performed using SPSS Statistical Package for Windows.

For each year, the positive mass increases recorded during each night were summated (SUM), following Ricklefs (1984). The maximum mass increase recorded in 2000 was 75 g. A minimum meal was defined as 10 % of this maximum meal to maintain an acceptable level of error (Phillips and Hamer 2000). Subsequently, therefore, an increase of 8 g was used to define a meal received during a 4 h interval, in 2000, 2001 and 2002. Analysis then focused on the weight loss experienced by nestlings before and after feeding. Unfed individuals were used to define inherent weight loss over time. Multiple Analysis of Covariance was used to determine how inherent weight loss was influenced by other factors, such as initial weight (PWEIGHT), burrow of origin (BURROW) and the size of an individual (BSINDEX), which reflects age. Rates of weight loss were considered as both linear and proportional functions of time ( $\text{g}\cdot\text{h}^{-1}$  and  $\log_{10}(\text{PWEIGHT}/\text{final weight})\text{h}^{-1}$ ). All of these factors, converted to a log scale, were best defined using inherent weight loss from unfed nestlings. The

methodology and analysis employed in this study matched that used in other studies (Ricklefs 1984a, Ricklefs et al. 1985, Hamer and Hill 1993, Bolton 1995, Hamer and Hill 1997).

It is important to correct for nestling size when determining the regression of weight loss on nestling weight, especially in species that breed asynchronously.

Hence, nestling size was introduced as a composite body size index as a covariate into the regression (Phillips and Hamer 2000). Z-scores of measured parameters such as head length, beak length and tarsus length were used. The analysis used in this study differs slightly from Phillips and Hamer (2000), since values for each of the parameters were log-transformed and a mean calculated. The mean for each parameter was then deducted from individual measurements for that parameter and divided by the standard deviation, giving the z-score for that individual. The z-scores were then summated for each individual. In contrast Phillips and Hamer (2000) log-transformed the summed z-scores rather than the original skeletal measurements.

Regression equations were developed to calculate weight loss between the initial and final weights determined each night, loss that occurred prior to feeding and after the consumption of food. The total amount of food delivered overnight (corrected meal size) to a nestling could then be calculated by correcting SUMs for inherent weight loss (CSUM). CSUMs were graphed to determine the amount of food needed to maintain a steady weight over a 24 h period (Hamer and Hill 1997). The resultant regression equation was later used to calculate the total amount of food delivered overnight throughout the nestling period, using daily morning weights. For Little Shearwaters the overnight food consumed by the nestling throughout ontogeny in

2000 and 2002 was used to comment on adult behaviour in years of different quality, along with the percentage of nestlings fed, based on 12 h weight differences and the average morning and afternoon weights recorded for the cohort over time.

Frequent weighing of Wedge-tailed Shearwater nestlings occurred over four consecutive nights on Lancelin Island from 11 to 15 March 2001 and on Rottnest Island from 16 to 20 April 2002. Nestlings were weighed at 4 h intervals at 17:30, 21:30, 01:30, 05:30 and 09:30 h WST. Previous studies suggest that the meal sizes and delivery rates in this species were not adversely affected by human handling of adults and nestlings (Baduini 2002).

The frequent weighing data were analysed as detailed in Chapter 4, however a larger meal size was defined for a larger species. The weight differences (uncorrected meal sizes) calculated over the 4 h intervals revealed that, for the Wedge-tailed Shearwater, ten percent of the maximum uncorrected meal size was 15 g. Consequently, 15 g was subsequently used to define a meal over a 4 h interval. In both years, the body size index derived from skeletal measurements of Wedge-tailed Shearwaters did not emerge as a significant factor for either fed or unfed nestlings. Nonetheless, body size index was incorporated in the analysis, using z-scores, to allow comparison with other studies which have found it to be an important factor (Phillips and Hamer 2000).

At Lancelin Island, Wedge-tailed Shearwater nestlings were weighed twice daily from 24 January to 03 May 2001, at 09:30 h and 17:30 h WST. The birds were visited at 09:30 h WST rather than sunrise (as was the case with the Little Shearwater), because of the need to swim to a moored dinghy and drive it to the island. Sampling did not



occur on the following days: 20-23 January, 20 February to 01 March, 10 March, 25-31 March, 01-03 April, and 19-24 April 2001.

In 2001, the total overnight food consumed by the nestlings throughout ontogeny was estimated from morning weights, using the regression equation derived from frequent weighing. This resulted in a real time sequence, which displayed the total food consumed by nestlings from 24 January until the whole colony fledged by May.

### 2.2.8 Adult activity during nestling feeding

Frequent weighing is generally only possible over a relatively short period of time and results obtained may reflect prevailing weather conditions. A longer term index of parental provision was thought and nestlings were weighed twice daily. The percentage of nestlings fed each night was determined using 12 h weight changes (Booth et al. 2002), with a 5 g weight difference over 12 h chosen to indicate a feed in Little Shearwaters. This was based on field experience obtained during frequent weighing. This minimum increase of 5 g between evening and morning weights (12 h period) differed from the minimum increase of 8 g used to define a meal over a 4 h period during the analysis of frequent weighing data. Over a 12 h period more time has elapsed in which to digest and metabolise the food, so that a smaller weight increase was deemed more appropriate. A positive increase in weight was used as an index of adult activity, because the assumption that an adult visit resulted in the consumption of a meal was observed to be true during frequent weighing. This indirect method was preferred to knock-down barricades, which were of little use on Beacon Island, as they were often bowled over by Bridled Terns competing for nest sites in early October.

Using 12 h weight differences, small meals may have been missed and this will be considered later. However, small meals, which cover maintenance needs, are even more likely to be missed using 24 h weight differences. In Little Shearwater, where a 5 g overnight increase in weight, recorded over a 12 h period, was found to underestimate the percentage of nestling fed by 5 % when compared to frequent weighing data (Chapter 4). However, frequent weighing data were more intrusive and time intensive to collect, and hardly suitable as a prolonged monitoring technique and it is easily biased by prevailing weather conditions. Consequently, although not perfect inferences about adult behaviour based on daily weight changes may contribute some interesting information.

For Little Shearwaters in 2000, morning and afternoon weights were obtained from 07 September to 22 October, 27 - 28 October, 04 - 05 November and 10 - 23 November. In 2002, they were taken from 07 - 22 September, 28 September to 06 October and 12 October to 18 November. For 2000 and 2002, the average morning and afternoon weights of nestlings were plotted over time to compare different years.

The percentage of Wedge-tailed Shearwater nestlings fed each night was determined by comparison of the afternoon and morning values obtained at Lancelin Island in 2001 throughout the nestling season and Rottneest in 2002 before fledging. Here 5 g was used to signal a meal over a 15 h period as daily weighing was conducted at 17:30 h and 9:30 h. 5 g was used based on experience in the field, and with consideration of metabolic and excretory loss of mass.

### 2.2.9 Stable isotope analysis

Stable isotope analysis of diverse materials was trailed to investigate the potential applications of the technique to indirectly study the foraging behaviour of pelagic seabirds at sea (Chapters 3, 6 and 8). This study was piggy-backed on an industry funded study to investigate the impacts of the Western Rock Lobster Industry of wedge-tailed shearwaters breeding efforts. It was found that discarded bait may subsidise breeding efforts of Wedge-tailed shearwaters at Lancelin Island, as these birds were observed to scavenge behind cray-boats (Dunlop and Asmussen unpublished). Extra materials were collected and prepared for analysis (Table 2.2).

**Table 2.3** The materials collected and prepared for stable isotope analysis.

Source of material	Sample size
<b>Wedge-tailed Shearwater</b>	
<u>Egg membranes:</u>	
Varanus Island	7
Rottnest Island	12
Airlie Island	2
Varanus Island	3
Serrurier	1
<u>Feathers from Lancelin Island:</u>	
Egg down	2
Secondary down	4
Plumage March	13
Plumage April	10
<b>Little Shearwater</b>	
<u>Egg membranes:</u>	
Beacon Island	7

Time-specific information about trophic levels, diet and foraging locations can be determined using stable isotope analysis of consumer tissue. Stable nitrogen levels reveal information about trophic levels (Hobson 1993, Hobson et al. 1994) and prey.

Between predator and prey, a step wise enrichment of 1-3 % in the ratio of stable nitrogen ( $^{15}\text{N}:$  $^{14}\text{N}$  is noted as  $\delta^{15}\text{N}$ ) isotopes of consumer protein occurs (deNiero and Epstein 1981 cited in Bearhop, 2001, Rau 1982 cited in Hobson et al. 1994). In contrast, the stable carbon ratio ( $^{13}\text{C}:$  $^{12}\text{C}$  noted as  $\delta^{13}\text{C}$ ) remains steady between predator and prey, and reveals the carbon pools accessed by the consumer. Carbon ratios can be indicative of foraging site as they can differentiate carbon pools, as for example between inshore and offshore food chains, (Hobson 1993, Hobson et al. 1994).

Since this is a pioneering application of the technique in Western Australia, reference material from specific sites has not been collated, thereby limiting interpretations.

This study aims to evaluate the potential application of the technique. In this study, the egg membrane compositions of Wedge-tailed Shearwater and Little Shearwater eggs were analysed to compare foraging behaviour between locations and species.

For this each egg membrane was separated from the shell, washed in distilled water, dried and stored in individual sealed containers. The egg membrane signatures were compared to that of potential prey targeted by the local purse seine industry (Chapter 3). Feather samples were also collected from nestling Wedge-tailed Shearwaters to monitor diet over time (Chapter 6) and egg membranes collected at different locations along the Western Australian coast were compared (Chapter 8).

The diet of Wedge-tailed Shearwaters over the breeding season at Lancelin Island was monitored from materials formed at different times. Egg membranes were collected after hatching in January, which would have been formed within the female during November (Chapter 8). The protoptile that developed within the egg in December or

early January was sampled from hatchlings in January. Feathers grown at different times after hatching were sampled. Mesoptile is grown in January and early February and tufts of it were removed from between the shoulder blades. Similarly, growing contour feathers were sampled in March and April. In March, feathers originated from actively growing scapular feather tracts; by April these feathers ceased growth and the actively growing coverts were collected instead.

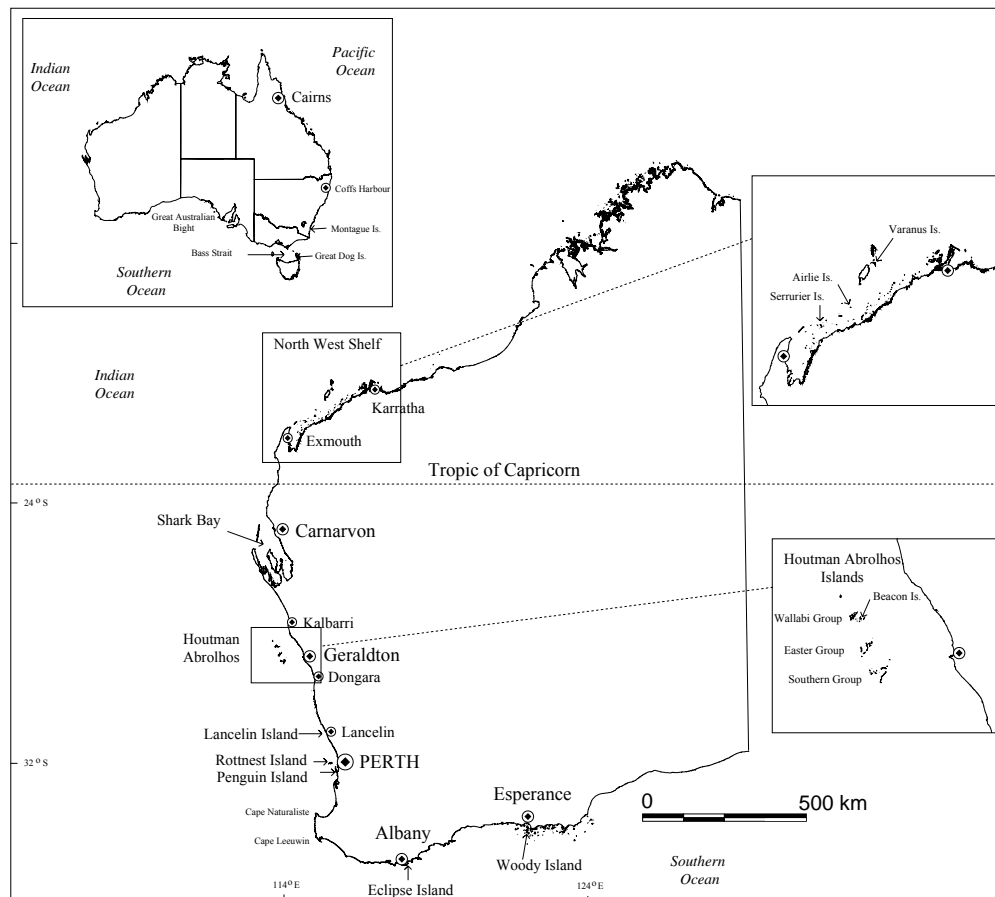
Both feathers and egg membranes were homogenised to allow subsampling, usually by grinding (Hobson 1995, Cherel et al. 2000); however, both stuck to the mortar and pestle. Re-hydration and subsequent drying of both materials was considered as impractical. As an alternative, both materials were cut into small pieces. Test runs revealed that an acceptable reading for both carbon and nitrogen isotopes were obtained from 2.5 - 3 g of egg membranes, and 2 - 2.5 g of Wedge-tailed Shearwater feathers. However, it proved extremely difficult to insert a sufficiently large amount of the non-conforming mesoptile into the tiny, sealed foil containers for analysis. Often an insufficient amount of protoptile had been collected from the small, vulnerable hatchlings, resulting in only a small number of samples analysed from nestlings at these stages.

The material were collected and prepared for analysis by the student and the stable isotope analysis was conducted by Lidia Bednark at the Botany Department of the University of Western Australia. Analysis followed standard continuous-flow isotope mass spectrometry procedures and statistical analysis to determine delta-13 carbon and delta-15 nitrogen composition (Thompson and Furness 1995, Cherel et al. 2000). This project was conducted in association with Dr Nic Dunlop and funded by Kailis

France (Lobster Australia) as applied research focused on the potential impacts on Wedge-tailed Shearwaters which have been observed to scavenge on bait discarded by the Western Rock Lobster fishery. The understanding of plumage growth in shearwaters developed during the research (Chapter 5 and 7) was used to target time-specific material formed by adult foraging effort at sea during different times of the breeding season.

### **2.3 Study sites**

The study was conducted at three different islands along the central Western Australian coast (Figure 2.2). The Little Shearwater was studied on Beacon Island (28° 28' 496" S, 113° 47' 091"E) at the Houtman Abrolhos Islands, at the northern limit of its distribution. However, reliable access to the remote study site for Little Shearwaters could not be assured outside the Western Rock Lobster fishing season (14 March to 30 June), which terminates before Little Shearwater nestlings hatch in winter or Wedge-tailed Shearwaters nestling hatch in summer. The Wedge-tailed Shearwater does not breed on Beacon Island, however it breeds in large numbers on many of the neighbouring Houtman Abrolhos Islands, especially at West Wallabi Island in the Wallabi Group (Marchant and Higgins 1990). Although, Wedge-tailed Shearwaters were studied at the Abrolhos Islands in the 2000 nestling season, the lack of reliable access resulted in the shift of the study to more accessible locations in future years.



**Figure 2.2** Map of Western Australia depicting the islands where most of the research was conducted (Beacon Island, Lancelin Island and Rottnest Island). Other locations frequently mentioned in the thesis are also shown.

Beacon Island is located 300 km north of Lancelin Island and 411 km north of Rottneest Island, where the Wedge-tailed Shearwater was studied in 2001 and 2002 respectively. In 2000, Wedge-tailed Shearwaters were also studied briefly at Pelsaert Island in the Southern Group of the Houtman Abrolhos Islands, where access to was intermittent and weather dependent, since the field site and accommodation (located at Fin Island) were on different islands, making it unsuitable for intensive research. Based upon this experience, the ideal study site for Little Shearwaters was Beacon Island, where the Department of Fisheries WA made available their camp.

### 2.3.1 Little Shearwater study at the Houtman Abrolhos

Little Shearwaters were studied in 2000, 2001 and 2002 on Beacon Island, in the Wallabi Group of the Houtman Abrolhos Islands. Beacon Island is one of the leeward Islands in the Wallabi Group situated to the east of Goss's Passage, which is up to 40 m deep. Beacon Island was visited in 2000 on the following dates: 26 June-02 July; 01 September until 23 October; 26-28 October; 03-04 November, 10-24 November. In 2001, it was visited in May, June, from August to September and early October. Thereafter, only incidental visits were possible to measure the birds. In 2002, the field season extended from 8 August to 17 November, with only brief absences to visit the mainland.

### **The Houtman Abrolhos Islands**

The three groups that form the Houtman Abrolhos Islands are located 60 to 90 km west of Geraldton and stretch from 28° 15' S to 29° 00' S, over a distance of 100 km. The island system is composed of three main reef platforms, running from the south to north, called the Southern Group, Easter Group and Wallabi Group. The three



platforms are separated by two channels over 40 m deep; the Zeewijk Channel in the south and Middle Channels further north. The system encompasses 122 islands, stretching over approximately 100 km. 22 islands are seasonally inhabited during the A Zone Western Rock Lobster *Panulirus cygnus* fishing season from 14 March to 30 June (WA Department of Fisheries 1998). Although vested in the Minister for WA Department of Fisheries the Abrolhos Islands are an A-class reserve (A 20253) for conservation, tourism and purposes ancillary to the fishing industry.

The Houtman Abrolhos Islands are located approximately 25 km east of the edge of the continental shelf, along which the Leeuwin Current runs southwards down the Western Australian coast. The Leeuwin Current transports low density, nutrient-poor, warm tropical water into southern reaches. It maintains water temperatures around the Abrolhos Islands at 20-22 °C throughout winter, allowing tropical marine organisms to flourish at latitudes where they do not generally occur (WA Department of Fisheries 1998, 2001). The strength of the Leeuwin Current is related to the Southern Oscillation (Pearce and Walker 1991) and the resultant La Niña and El Niño years have marked influences upon the oceanic resources and breeding activities of seabirds along the Western Australian coast (Wooller et al. 1991, Integrated Shearwater Monitoring Program 2001, Surman 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, Surman et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006). The presence of a warm Leeuwin Current results in many tropical and subtropical bird species breeding further south on the western coast than on the eastern coast of Australia (Burbidge and Johnstone 1993). As a result, the Houtman Abrolhos is one of the most important breeding sites for seabirds along the Western Australian coast (Wooller et al. 1990, Burbidge and Johnstone

1993, Surman 1997, 2001, Surman et al. 2002), however to date its value for marine raptor conservation has not been formally acknowledged.

Beacon Island has a maximum length of 350 m and is 150 m at its widest point. Its maximum height above sea level is less than 2 m. Weather data was to be sourced from the weather station on North Island also in the Wallabi Group, at approximately 20 m above sea level. However, due to frequent failure and low repair priority outside the Western Rock Lobster season, wind speed and direction were also measured at Beacon Island. Barometric pressure available for North Island was compared to the more reliable station at Geraldton, on the mainland, demonstrating only a small time lag detected between the two sites. Consequently, barometric pressure was sourced from Geraldton airport, but not wind, since this is greatly influenced by the mainland.

Like most islands in the Abrolhos, Beacon Island is of coralline origin. It is a coral storm-ridge island with a central deposit of sand and halophilic plants (*Atriplex*, *Nitraria* sp.) (Collins et al. 1991, Collins et al. 1998). It is surrounded by aqua-coloured, sandy shallows, which are dotted with mazes of branching and plate *Acropora*. This platform gives rise to the south and east to Morning Reef, and surfaces at the east end as a chain of islands composed of Seal, Dakin and Easter Islands. To the west, at the edge of the island, the coral platform suddenly drops off to a depth of 40 m into Goss's Passage that allows safe and easy passage through the group. Pelagic fish and cetaceans travel through this passage and Wedge-tailed Shearwaters often congregate there before dusk, to visit Long Island and Dicks Island.

### 2.3.2 Seabird populations of the Houtman Abrolhos

Conventionally seabirds breeding at the Houtman Abrolhos Islands have been divided into “burrow-nesting” and “surface-nesting species” for management purposes. The Wallabi Group provides nesting habitat for three burrow nesting species including Wedge-tailed Shearwaters, Little Shearwaters and White-faced Storm-Petrels *Pelagodroma marina*. Surface-nesting seabird species include Bridled Terns, Roseate Terns *Sterna dougallii* and Crested Terns *Sterna bergii*, whilst the Lesser Noddy, Common Noddy and Sooty Tern do not appear to regularly breed in the Wallabi Group, although prolific breeders in the other groups. The Wallabi Group is also one of the most important breeding sites for White-bellied Sea-eagles *Haliaeetus leucogaster* and Osprey *Pandion haliaetus* along the Western Australian coast with 18 breeding pairs and 19 breeding pairs of each species respectively recorded in 2002 (pers. observations).

Most seabirds, including the Little Shearwaters and Wedge-tailed Shearwaters are predated by White-bellied Sea-eagles. At the Abrolhos Islands, the breeding season of Little Shearwaters and White-bellied Sea-eagles overlap, whilst most other species of seabirds initiate reproduction in the summer months, when winter breeders have mature nestlings. The summer breeding seabirds provide continued resources to support the reproductive efforts and persistence of territorial White-bellied Sea-eagles.

Beacon Island is used as a breeding site by at least five species of seabirds including two burrow-nesters and three surface-nesters, whilst two terrestrial species also appear to breed there, the Silvereye *Zosterops lateralis* and the Spotless Crane

*Porzana tabuensis*. Burrow-nesting birds utilise sandy areas nearly all year round. White-faced Storm-Petrels, return in late June for pre-breeding activities and have nestlings in November that fledge in January. The White-faced Storm-Petrel digs long twisting, convoluted burrows with a neat, fist-sized spherical entrance. They breed on Beacon Island, but also on adjacent leeward Islands, including Long Island, Seal Island, Eastern Island and Dakin Island. At some of these sites nestlings are quite accessible, since the soil is often shallow on young islands.

Little Shearwaters are known to be present from March to early December and their burrows have larger entrances. Little Shearwaters have also been observed to use bush burrows where the soil is shallow over coral rubble. Wedge-tailed Shearwaters do not breed on Beacon Island, but utilise the adjacent Long Island and Dicks Island. They often forage in Goss's Passage and in the deeper waters north of Beacon Island. The largest breeding colony of Wedge-tailed Shearwaters, found on the central west coast, is located on West Wallabi Island, along with a colony of Little Shearwaters and White-faced Storm Petrel (Fuller et al. 1994).

Surface-nesting birds on Beacon Island include a large colony of Bridled Terns and Roseate Terns which breed in large numbers in autumn, but a small number also attempt to breed in spring on the south-eastern tip of Beacon Island. Here, a solitary pair of Pacific Gulls *Larus pacificus* breeds in spring. Spotless Crakes have nestlings in September/October and adults appear to predate Little Shearwater eggs. Surface-nesters generally lay camouflaged eggs, which can easily be trampled. If breeding colonies of surface-nesting seabirds are disturbed by humans, predation of eggs by the more tolerant Silver Gulls *Larus novaehollandiae* can occur. Silver Gulls breed on

the adjacent Long Island during autumn and scavenge on discarded bait from the Western Rock Lobster fisheries, which may artificially increase their breeding efforts.

Marine raptors use Beacon Island and the surrounding shallows to forage. Ospreys and White-bellied Sea-Eagles currently breed on the adjacent islands, including Long Island, Eastern and Traitors Island. Ospreys once bred on one of the jetties on the south-western side of Beacon Island, on top of a stack of old beehive cray-pots, which were removed to replace sections of a jetty. Similarly, White-bellied Sea-eagles used to breed on the northern jetty on top of a fuel tank that was removed. Species such as the Osprey, White-bellied Sea-Eagle, Crested Terns, Pied Oystercatcher *Haematopus longirostris*, Eastern Reef Egrets *Ardea sacra* and Ruddy Turnstones *Arenaria interpres* regularly use the island and surrounding shallows to rest or forage.

### 2.3.3 Wedge-tailed Shearwater study sites

Wedge-tailed Shearwaters were studied on Pelsaert Island in 2000, Lancelin Island in 2001 and on Rottnest Island in 2002 (Figure 2.2) to facilitate reliable access to colonies and research support. Wedge-tailed Shearwaters were initially studied on Pelsaert Island in the Southern Group of the Abrolhos Islands in 2000. Further studies in the Houtman Abrolhos Islands were rejected as access was difficult and irregular, although they breed in extremely large numbers on West Wallabi Island and in small numbers on Long and Dicks Island (Burbidge and Fuller 1993). Instead, more readily accessible study sites were chosen, such as Lancelin Island in 2001 (Figure 2.2). In 2002, Rottnest Island (Figure 2.2) was visit, because it was easier to conduct respirometry experiments there, in collaboration with Professor Phil Withers from the University of Western Australia. Wedge-tailed Shearwater research was

designed to target specific areas of interest, whilst the Little Shearwater was the focal species of the study.

#### 2.3.4 Lancelin Island

Lancelin Island (31° 00' 27" S, 115° 18' 56" E) is part of the Turquoise Coast Island Nature Reserves that includes 38 limestone islands stretching from Lancelin (110 km north of Perth) to the Beagle Island group (260 km north of Perth). Lancelin Island is 8.2 ha and located 0.6 km from the mainland, with a maximum elevation of 27 m (Ford 1965, CALM 2001). The proximity of the island to the coastal town of Lancelin, a popular holiday destination, gives rise to diverse management issues stemming from visitation. Lancelin Island is an A-class nature reserve (A 24979) and the extensive reef system to the west became gazetted as a Fish Habitat Protection Area in 2001, through community initiative. Lancelin Island is used as a breeding site by several seabird species, including some whose range has extended southwards (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001). Three species of burrow-nesting seabirds breed on Lancelin Island, namely Wedge-tailed Shearwaters, White-faced Storm Petrels and about 30 pairs of Little Shearwaters. The presence of Little Shearwaters breeding in *Nitraria billardierei* at the western beach was discovered in April 2001, whilst undertaking night work for this study.

Surface-nesting birds also have a long breeding association with the island, and include large numbers of Bridled Terns, Roseate Terns, Crested Terns, Fairy Terns *Sterna nereis*, as well as some Caspian Terns *Sterna caspia* and Pacific Gulls. The Bridled Terns arrived in the early 1960s and now breed there in the thousands. More recent arrivals are subtropical species that are extending their range southwards, including a now well-established colony of Common Noddies (arrived 1992) and a

small colony of Sooty Terns which began to breed in the 1997/98 breeding season (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001). Recent breeding attempts by Fairy Terns have been unsuccessful, possibly owing to human disturbance.

Birds of prey visiting the island varied seasonally and only Ospreys used it as a breeding site. Occasionally, a White-bellied Sea-eagle visited Lancelin Island to prey on birds. Other, raptorial visitors from the mainland are the Australian Kestrel *Falco cenchroides* and Black-shouldered Kite *Elanus notatus*. Peregrine Falcons *Falco peregrinus* hunt Bridled Terns during their breeding season and swoop upon aggregations of Pied Cormorants *Phalacrocorax varius* on the northern end of the island. Little Eagles *Hieraaetus morphnoides* predate Wedge-tailed Shearwater nestlings prior to fledging. A Barn Owl *Tyto alba* was also seen. This suggests that raptors are attracted by the predictable occurrence of breeding seabirds.

### 2.3.5 Rottnest Island

Wedge-tailed Shearwaters were also studied on Rottnest Island (32° 00'S, 115° 29'E), a limestone island located 18 km west of Fremantle (Saunders and de Rebeira 1993). It is the most westerly island in a semi-submerged limestone ridge, which includes Carnac and Garden Islands. The island is relatively large (1900 ha), 11 km long and 4.5 km at its widest point. It is an A-class recreational national park (A16713) and is a popular tourist destination, attracting about 300 000 visitors in 1990 (Rippey and Rowland 1995), being serviced by regular ferries from Perth. On Rottnest Island, visitors' travel is restricted to walking, bicycles and buses. Most human habitation and activity is restricted to the eastern and north-eastern part of the island.

The island is orientated approximately east-west, with shearwater colonies at West End (Cape Vlamingh, Cathedral Rocks, Radar Reef) and two smaller colonies further east, along Strickland Bay. Historical records suggest that the Wedge-tailed Shearwater population on Rottneest Island has increased dramatically to present levels (Bancroft et al. 2004). The research was conducted at Cape Vlamingh (32° 02'S 115° 27'E), at the south-western extreme of the island with a maximum height of 37 m above chart datum. Accommodation was provided by the Rottneest Island Research Station, located at 45 m above sea level, next to the Rottneest lighthouse and weather station. Birds of prey seen on the island include Ospreys, Black-shouldered Kites, Australian Kestrels and the occasional Swamp Harrier *Circus approximans*, while Boobooks *Ninox novaeseelandiae* and Barn Owls were seen at night.

Burrow occupancy at Cape Vlamingh was monitored in late December during 2000 and 2001, and again throughout most of January 2002 to record hatching success and sequence of hatching. This produced nestlings of known ages and provided the basis for subsequent research in April-May 2002. As on Lancelin Island, areas used intensively by breeding Wedge-tailed Shearwaters, are dominated by colonising plants, such as Iceplant *Mesembryanthemum crystallinum* and Pigface *Carpobrotus virescens*. Here burrows are less stable over time than in areas covered by plants with deeper root systems.

### 2.3.6 Climate

The climate on the Western Australian coast is greatly influenced by the Leeuwin Current, which flows most strongly between March and October, and whose strength varies between years. Through the presence of this warm current running down a western seaboard, the climate along the lower Western Australian coast is warmer and



wetter than at other locations with a similar latitude within the southern hemisphere (Rippey and Rowland 1995). Naturally, the presence or absence of large volumes of south-flowing, warm water affects the passage of weather systems and the resultant rainfall potential.

On the Western Australian coast, rainfall varies with latitude, with winter rains experienced further south and summer rains in tropical regions. Within the study area, winter rain falls mainly between May and August, dependent mainly upon the extent to which fronts sweep northwards from the southern oceans. Summer showers are infrequent, but can result from the southern passage of dissipating tropical lows. Only infrequently do summer rains travel sufficiently far south, being dependent upon the severity, longevity and path of an unpredictable system. Most dissipating tropical lows are associated with low winds and cloud cover, but do not bring rain. The mean annual rainfall within the study area was highest at the southernmost islands, Rottnest Island (717 mm), and Lancelin Island (639 mm) (Rippey and Rowland 1995), while rainfall was lower further north, with 469 mm of rain registered as an average for the Abrolhos Islands (WA Department of Fisheries 1998).

In summer, the winds along the western coast of Western Australia are dominated by early offshore winds and afternoon sea breezes. The summer southerlies intensify northwards from Cape Naturaliste towards Exmouth, when the axis of the summer highs lies along 35-40 °S (Laws 2001). At the Abrolhos Islands, the winds in summer are dominated by strong SE and SW winds, 76 % of which exceed 20 kmh<sup>-1</sup> and 44 % of which exceed 32 kmh<sup>-1</sup>. During the winter months, especially in July and August, calm conditions can prevail, usually preceding frontal activity (WA Department of

Fisheries 1998, 2001). In winter, the band of high pressure cells shift north to 25-30° S. In winter, cold fronts intensify and travel further north, with the tail end of intense fronts reaching as far north as Exmouth. Cold fronts arrive from the west or south west. Bad weather is associated with these lows and their arrival is signalled by winds veering north and then north-west when the front hits (Laws 2001). Wind roses for each study site are given in Chapter 1 (Figure 1.1, 1.2 and 1.3).

Weather information was recorded at Beacon Island to supplement meteorological data sourced from the Bureau of Meteorology. Given the flying capability of seabirds the weather experienced at the breeding location does not necessarily match that of the foraging site. However, along the western seaboard foraging locations can only be located to the west of the continent, and weather patterns predictably move from west to east (section 1.4). Consequently, weather patterns at the breeding colony or at a weather station of similar latitude may reflect travel conditions utilised by seabirds or give an indication of large scale weather changes associated with the predictable movement of a weather system from the west to the east, albeit with a time lag. The use of time lag in statistical analysis (cross correlation frequency analysis in Chapter 3 and 4) and the documentation of weather condition used by birds during travel to arrive at the breeding location may give some insight into the behaviour of seabirds.

## **3 Chapter 3: The nesting, pairing, incubation and hatching behaviour of the Little Shearwater**

### **3.1 Introduction**

This chapter focuses on the early phases of parental provisioning in Little Shearwaters namely the pre-laying season, the incubation period and transition to nestling feeding, which may impact on nestling feeding monitored in Chapter 4. The breeding site is described and breeding participation is compared between years. The weight recorded for adults at the colony are compared whilst engaged in different phases of the reproductive cycle and in different years. Patterns of adult attendance patterns are examined, including the duration of incubation shifts and adult weight loss experienced during incubation shifts. The interaction between weather and the temporal patterns of provisioning during the incubation phase and during the transition phase to nestling feeding will be examined. Stable isotope analysis will be used to comment on female Little Shearwater foraging during egg membrane formation. Hatching was monitored to determine the spread of hatching dates within the colony on Beacon Island. The duration of the guard period and weight gain by nestlings after hatching is also discussed.

#### **3.1.1 Importance of pre-laying and incubation behaviour**

Parental provisioning starts before the hatching of the nestling and includes pre-laying behaviour and incubation. Each stage of the breeding cycle acts like a filter phase and may entrain or influence future patterns of provisioning. During the pre-laying period pair formation, bond strengthening, burrow building and mating occur. Thereafter,

females need to be able to devote energy and nutrients to form the egg, a process that generally occurs during a prolonged absence from the colony (Warham 1990, Brooke 2004). For example, at Rottneest Island, the whole Wedge-tailed Shearwater colony engages in a complete exodus during which both females and males are absent (Garkaklis et al. 1998). Females then return to lay an egg and incubation commences. Stable isotope analysis of egg membranes were used to comment upon the foraging of female Little Shearwater during egg formation.

During the prolonged period of incubation (Boersma 1982, Ricklefs 1984b), biparental care is necessary to ensure development of the Procellariiform nestling. For shearwaters, incubation and foraging are mutually exclusive events and incubation shifts are often of long duration (Brooke 2004). As a result, incubation is costly for adults (Minguez 1998) and there are limits to the duration of fasting. If a bird is not relieved by its partner, it is thought that the incubating adult will terminate an incubation stint when a threshold body weight is reached, which may differ between individuals (Chaurand and Weimerskirch 1994a). Iteroparous, long-lived organisms, such as shearwaters, would be expected to protect adult body condition in order to optimise their future reproductive potential (Minguez, 1998; Stearns, 1992), as detailed in Chapter 1. In this chapter, the weight loss of adult Little Shearwaters during incubation shifts will be documented and may provide some insight into decision making and threshold weights.

The unattended egg, although resistant to prolonged chilling, may be predated (Warham 1990). Hence, the partner foraging at sea should return in time to relieve the incubating mate to ensure continuous attendance and minimise predation risks.

Adults thus need to maintain their body condition while co-ordinating their efforts to maintain a viable egg. The temporal patterns adopted during the incubation phase may well set the temporal pattern later adopted by parents during food delivery to nestlings (Brooke 2004). It is therefore important to view provisioning patterns in the context of the whole breeding season, rather than in isolation. Consequently, temporal patterns of provisioning were documented on Beacon Island in 2002, during late incubation and the transitions to food delivery to nestlings using a nocturnal survey method.

### 3.1.2 Breeding synchrony

Shearwaters breed over a large range of latitudes and the timing of events can vary greatly between and within species (Warham 1990; Brooke 2004). It has been suggested that breeding synchrony may reflect how long resources are able to support reproduction near a given breeding site and how tightly packaged events are within the annual (or biennial) cycle of a species. For example, at high latitudes, where resources are only available for a limited period, breeding is often a highly synchronous event. Once resources crash, birds such as Short-tailed Shearwaters must migrate to other areas of productivity (Warham 1990).

At lower latitudes the absence of temporally constrained resources allows breeding to occur over a longer time span (Brooke 1990). Generally, tropical environments are associated with low levels of resources that are available over a long period of time, and lack the predictable peaks in productivity characteristic of high latitudes (Warham 1990; Brooke 2004). Shearwaters are colonial breeders and competition for resources near the central breeding site inevitably peaks with breeding activity. Asynchrony

could spread resource use by the colony over time and thereby reduce competition. Asynchronous reproduction would be suited for colonies of Wedge-tailed Shearwaters and Little Shearwaters breeding in mid to low latitude waters off the Western Australian coast.

A reduction in synchrony has also been linked to size, since smaller species take a shorter time to breed and it would seem easier to fit all events into the year (Brooke 1990). However, relatively speaking, incubation and the rearing of nestlings occurs at a slower rate in smaller than in larger birds. The Little Shearwater, as the smallest of the *Puffinus* shearwaters breeding at low latitudes, might therefore be expected to show less synchrony than larger congeners, especially if breeding at higher latitudes.

## **3.2 Methods**

### **3.2.1 Monitoring of burrows**

To minimise disturbance during incubation and brooding, most burrows were only monitored using a burrowscope to observe adult attendance, hatching dates and the duration of the guard period. However, a small number of burrows were monitored more intensively. In 2001, incubating birds and eggs at 10 burrows were weighed daily during late incubation. The repeated handling of eggs and disturbance to adults over a longer period of time are believed to have adversely affected breeding success and may have altered the duration of incubation shifts. Subsequently, in 2002, disturbance was minimised to determine the duration of incubation shifts. Adults were only weighed on arrival and marked on the white neck and breast using a waterproof pen. The mark was placed so that the bird could not preen the marked site. On subsequent days, the bird with the mark could be identified using the

burrowscope, without the need to handle it. This mark persisted on the incubating bird, whilst a bird returning from sea carried at most a faint mark. As a result, disturbance of incubating birds was minimal, which enabled the monitoring of the length of incubation shifts. Incubation change-overs were defined as the arrival of a different adult, which usually, but not always, defined the length of the incubation shift.

During the guard period, disturbance to monitored burrows was also minimised in 2002 in order to determine accurately the time for which a nestling was brooded continuously. Here only the absence or presence of an adult was noted using a burrowscope. Therefore, adults were not identified and not all nestlings were measured when first hatched. Instead, nestlings were opportunistically measured and weighed when not attended by an adult during the day. Once the guard period had ended, nestlings were weighed twice daily and measured at regular intervals to track growth.

### 3.2.2 Nocturnal activity surveys

Cray-fishing families inhabit the islands from 15 March to 30 June. Feedback from resident fishermen on Beacon Island suggested that throughout this period Little Shearwaters are active on the island, although nocturnal activities vary over time (Craig Culliver 2000-2003, pers. comm.). It was considered important to document adult activity during incubation and the transition to nestling feeding. During this time it was chosen not to handle and disturb incubating birds in burrow nightly, as a small sample size ( $n=10$ ) in 2001 appeared to be adversely affected. Consequently an indirect technique was used. Pop-sticks or other barricades were of limited use, as

incubating birds often left the burrow to vocalise outside the burrow and later to re-enter the burrow to incubate, without a change-over having occurred. Furthermore, whilst living at the island it was attractive to investigate if fluctuating call activity could be utilised as an index of bird activity. Fluctuations in nocturnal activity were examined, firstly to see if audible fluctuations in call activity could be used to approximate arrival and departure activity and secondly if fluctuations in activity were related to weather.

Nocturnal survey technique was developed to document these peaks and ebbs in the nocturnal activity of adults in a manner that was to reflect changes in activity, be repeatable and suitable to conduct over a prolonged period of time. Therefore, it required to be rapid to conduct, not exhausting or involve changing to field work clothes and with minimal impact on birds. During each sampling bout, two nocturnal activity surveys were completed along a set path in the evening and again in the morning, about 1.5 hours after sunset and before sunrise, in the middle of the dawn departure chorus. Call activity was recorded along a set path approximately 120 m long, located within the colony (Figure 3.1). An index of adult activity was created by recording vocalisation and also the number of birds observed flying during each nocturnal survey. The results of the two nocturnal activity surveys conducted in the evening and morning were averaged to obtain one evening and one morning measure of Little Shearwater activity for each date. These nocturnal surveys were conducted during incubation and in the transition phase to nestling feeding from 13 August until the 22 September 2002.



During the nocturnal surveys, firstly the call activity was recorded along a 5 minute transects. A call from an individual can be composed of a string of “Wah-i Wah-i Wah-i” followed by a terminating “Wah-ooo” (Serventy et al. 1971). All Little Shearwater vocalisation heard on the ground and in the air was counted, with each syllable (Wah-i and Wahoo) counted separately. Two transects were conducted, and the number of calls counted during each of the two 5 minute transects was later averaged. Since, calls uttered by birds in flight as well as on the ground were both recorded, birds already present on the island, possibly incubating, were also included in the survey. Secondly, the number of Little Shearwaters observed to be flying were counted at a central location within the colony, at the end of the transect, during two one-minute sampling intervals, and this was also averaged.

It was thought that the birds counted in the evening would reflect arrival activity, whereas the birds seen flying before dawn would reflect departure activity. As a reference, the spot surveys did mirror the changes in nocturnal activity heard on the island, whilst living in the middle of the colony of active Little Shearwater burrows. If a White-bellied Sea-eagle was present, the behaviour of Little Shearwaters may have been altered, especially near civil dusk, by the presence of a predator. However, the presence of an observer generally displaced the predator. Nonetheless, surveys were conducted in the dark to correct for predator activity. The survey was conducted from 13 August 2002 to 22 September 2002, and from 28 - 31 September 2002. This encompassed late incubation, hatching (starting at the end of August), brooding and the transition to nestling feeding.

The relationship between incubation change-overs and weather was explored using cross correlation frequency, performed by SPSS Statistical Package for Windows. A similar analysis was used to examine the cross correlation frequencies between parameters recorded during the nocturnal surveys and weather. Weather variables tested included the morning and evening pressure, morning and evening wind direction and speed, and 24 h pressure differences.

The weather was recorded at Beacon Island and also supplied by the Bureau of Meteorology. 24 h pressure differences were calculated between the evening pressure readings on two consecutive days. A drop in pressure was associated with the passage of a front. In winter, the approach and passage of a front resulted in an anticlockwise veering in the direction of the wind. Prior to its arrival north east winds prevailed that swung to the north-west ( $315^\circ$ ) on arrival of the front, then west and later south west with the passage of the front. Cross-correlation analysis was performed using a seven-day time lag. Only for pressure and 24 h pressure difference was it possible to include weather information for seven days before and after the sample period; such information was not available for wind speed and direction.

Data from the North Island weather station were sparse and erratic. However, when operable the barometric pressure at North Island matched the pressure in Geraldton, allowing pressure data to be sourced from the Geraldton Meteorology station. In contrast, the wind experienced at the mainland often differed greatly from that at the islands, in both magnitude and direction, especially in the morning. Hence, it was necessary to record the weather twice daily at 05:30 h and at 17:30 h using a hand-

held anemometer whilst standing on the northern jetty at Beacon Island. The wind direction was estimated to the nearest 1/16 of 360° from a fixed spot.

### 3.2.3 Sexing of adult Little Shearwaters

Both adults incubate and subsequently have brood patches. During the monitoring of incubation shifts, it was assumed that the larger member of the pair was the male. However, size dimorphism between partners was often small, making it difficult to tell them apart. Although other methods were explored, for example males appeared slightly larger than females in the soft tissue area around the nape and neck, these proved difficult to quantify. Feathers from adults and their nestling have been collected for future DNA analysis.

## 3.3 Results

### 3.3.1 Burrows and burrow attendance during the pre-laying season

The areas used by Little Shearwaters and White-faced Storm Petrels were covered with enough soil to dig tunnels (Figure 3.1), except for a small area west of the camp built by the Dransfield family (fifth and sixth dwelling from the north). Here, coral shingles were frequent and Little Shearwaters laid their eggs under bushes, although this was only observed in 2000 when breeding participation was high. Approximately 50% of nests monitored in this study were tunnel-burrows located near previously disturbed areas, such as old paths and dump, to minimise damage to fragile, arid vegetation. To remove bias and to maintain a sufficient sample size of accessible burrows, a previously undisturbed area south of the school (fourth building from the

southeast) was also monitored, where disturbance to the vegetation was less visible to the public. This was advisable, as repeated visits did damage vegetation. Old scars from disused paths used in the 1960's are still visible on aerial photographs.

Most burrows were dug under large *N. billardierei* bushes that often reached 1.5 – 2 m in height and covered large areas of the island. As a result, about 70 % of the colony was not accessible without heavily disturbing the vegetation. Arriving Little Shearwaters crashed into the vegetation and slipped down between branches to access the ground. Others landed on nearby paths and scurried under the bushes. Upon departure, birds climbed up through the branches and launched themselves off elevated positions. Most entrances of accessible burrows in the areas dominated by *N. billardierei* were located at the edges of paths and buildings, or in areas covered by less dense, colonising vegetation.

The vegetation cover (Figure 3.1) reflects soil depth. The north-eastern areas of the island are dominated by the edible Sea Grape *N. billardierei* bushes, where the soil is deeper, darker and the composition of coral rubble is lower. At the north-western and western end of the island, white coral rubble builds up during storm surges and inland areas are composed of leached, grey-discoloured and brittle coral shingles. Further inland, the substrate is composed of greater proportions of soil, but still retains some coral rubble and supports Grey Saltbush *Atriplex cinerea*, *Myoporum insulare* and some Coast Bonefruit *Threlkeldia diffusa*. As the percentage of soil and its depth increase towards the centre of the island, so does the cover by *N. billardierei*. Along the south-facing sandy beach, the sand is white and deep, and continues inland to the area covered with camps. The centre of the island is covered in colonising vegetation,

**Figure 3.1** The distribution of four species of seabird breeding sites on Beacon Island in relation to soil depth and vegetation.

whilst large *N. billardierei* bushes grow at the edge of the south-facing beach and cover extensive areas running northwards along the western reaches of the central section of the island.

Human structures may have altered the vegetation structure of the island, as evidenced by extremely large bushes of *N. billardierei* near camps. The bushes appear to have increased to their present height after the erection of the fishing camps on the island, which deflect the wind, provide shelter, collect and retain moisture. These areas are inaccessible to humans, but provide habitat to breeding Little Shearwaters, which fertilise them. This may have increased the structural integrity of the burrow, through developed roots and the presence of concrete slabs, possibly removing the need to dig new burrows in different years.

In the area adjacent to the path leading to the old, western jetty on the south side of the island, white sandy soil prevails that supports less dense vegetation of lower height and of colonising nature. These areas are exposed to the prevailing southerly winds and are predominantly used by White-faced Storm Petrels. Some Little Shearwater burrows can be found here and are often associated with isolated patches of *N. billardierei*. In adjacent areas, the densities of Little Shearwaters increase with the increased presence of *N. billardierei*. Many Little Shearwaters breed in the area adjacent to the school. Here large patches of *N. billardierei* exist, which partially exclude human access. However, these patches are invaded by areas of white sandy soil, which are dominated by *A. cinerea* and *M. insulare* bushes, and allow partial access. The distribution of burrow nesters is largely determined by soil depth,

composition, which also affects vegetation cover, while the distribution of surface nesting birds is more even (Figure 3.1).

Two types of nests were used by Little Shearwaters on Beacon Island, tunnel burrows and bush nests. Tunnel burrows were mostly surveyed in this study. Their dimensions varied considerably, especially in length (Table 3.1).

**Table 3.1** The mean ( $\pm$  S.D.) dimension of 42 Little Shearwater burrows monitored on Beacon Island.

	Burrow entrance		Burrow Length (cm)
	Width (cm)	Height (cm)	
Mean	15	9.4	55.4
S.D.	$\pm 2.5$	$\pm 2.2$	$\pm 55$
Minimum	11	5	18
Maximum	12	15	250

Many burrows were too long to access the nesting chamber with ease (i.e. longer than 0.75 m). These were monitored with a burrowscope during incubation. However, in 2001, malfunction of the burrowscope reduced the number of burrows surveyed for hatching from 53 to 38. To monitor nestling growth, when burrows were too long, a second entrance was often dug, after the termination of the guard period and covered when not in use.

Bush nests occurred in areas where too many coral shingles within the soil made digging difficult. Instead, the eggs were laid in a bush and many above-ground tunnels existed within the vegetation were monitored to access nesting chambers. Bush nests were difficult to find. In 2000, a playback recording of nestling begging calls was used successfully to find bush nests by eliciting begging calls from hidden nestlings. These surface nests were more susceptible to the weather than sub-surface

burrows, as nestlings were wet after rains. Only ten bush nests were included in the study in 2000. These were included to remove bias towards soil burrows. These burrows were not monitored during period of heavy rains or when the vegetation was wet, so as not to further disadvantage already wet nestlings. It was not known if the pairs using bush burrows were of marginal quality compared to ones able to claim a patch in the centre of the colony, where a layer of soil protected the nestling from the elements. However, in 2000, the use of bush nests appeared to be more prevalent, whilst in 2001 and 2002, years of decreased breeding participation, no nestlings were encountered in bush nests despite the use of playback of nestling calls to locate bush burrows.

In the pre-laying period, from 28 May to 08 June 2001, Little Shearwater burrows were monitored during the day. Of 943 burrow inspections during the day, adults were present on 2.8 % of occasions. At those burrows occupied during the day, two adults were present on 55.4 % of occasions. Knock-down barricades revealed that 38.1 % of burrows were visited by at least one bird during the night. Later, from 18 to 28 June 2001, during 950 burrow inspections, no adults were present during the day. However, barricades erected before the entrance indicated that, during the night, 49.3 % of burrows were visited by at least one bird. Nightly attendance at burrows fluctuated markedly (Figure 3.2).



**Figure 3.2** The percentage of burrows visited by Little Shearwater during each night indicated during the pre-laying season on Beacon Island in 2001.

In 2000, from 28 June to 02 July, the weights of two individuals monitored during several consecutive days dropped sequentially. Bird 1 dropped from 181 g to 171 g over two days and then to 164 g on the third day; bird 2 decreased from 175 g to 155 g. However, it was not known if the first day they were monitored represented the first day that they did not return to sea to forage. Another bird, when first encountered during the day weighed 170 g, was absent during the next day, but was present the day after with a weight of 159 g. Morphometric measurements suggested that the birds present during the day were quite large, and possibly males.

Of the 101 different burrows occupied by adults at night at different times in the pre-laying stage, only 28 % of burrows contained an egg by mid August 2001, towards the end of the incubation period. Hence, burrow occupancy during the pre-laying season did not accurately predict subsequent participation in reproduction. Whilst, establishing the annual research burrows efforts used to locate burrow with eggs or nestlings were recorded. Initial search efforts suggested that in 2000 at 71 % burrow (n= 100) investigated contained an egg or very young hatchling, whilst in 2001 42 % burrows (n= 150) contained an egg. In 2002 it was even more difficult to locate breeding attempts as only 31 % burrows (n= 170) investigated for content contained an egg. Not all burrows could be monitored during nestling feeding, as burrows were often too long or located in sensitive vegetation. Additional burrows containing a nestling to be monitored during parental provisioning were located with time.

Most burrows were visited by two adults during the pre-laying period and whilst feeding nestlings (Table 3.2). However, one or two other individuals were found in a

burrow, in addition to the regular pair attending the nestling; in 45% of these burrows attended by more than two adults, a nestling was reared.

**Table 3.2** The number and percentage of Little Shearwaters recorded in a burrow based on band numbers.

Number of different birds encountered in a burrow	Frequency (%)			
	Pre-laying	Nestling feeding		
	2001 (%)	2000	2001	2002
2	31 (84)	14 (78)	17 (81)	17 (74)
3	3 (8)	0	3 (14)	5 (22)
4	3 (8)	4 (22)	1 (5)	1 (4)

Although, most burrows did not survive consecutive breeding seasons, a small number persisted between years, and some individuals were located in the same burrow in subsequent years. In 2000, 51 pairs of adults and their nestlings were banded. The same burrows were checked in 2001, but many were disused or had become too long to monitor. Eight individuals were with the same partner in the same burrow. Five individuals were in the same burrow, but with a different partner.

### 3.3.2 Egg membrane composition

The stable isotope analysis of egg membranes formed by Little Shearwater females from Beacon Island yield values that were not clumped (Figure 3.3). Stable isotope analysis of egg membranes suggested that during egg formation most Little Shearwaters feed at a low trophic level similar to that represented by bait-fish, such as the Scaly Mackerel *Sardinella lemuru* which were purse-seined off the central west coast. Nonetheless, this was not a universal trait, as indicated by a few Little Shearwaters, which fed at a much higher trophic level.

**Figure 3.3** The delta-13 carbon and delta-15 nitrogen composition of Little Shearwater egg membranes.

### 3.3.3 Adult weights during the early phases of provisioning

The body masses of 194 adults were recorded in the pre-laying season from 28 May to 25 June 2001, when birds were excavating burrows, forming pair bonds and mating. Forty adults were also weighed in late June in the preceding year. Despite differences in sample size in the two years, mean weights were similar (Table 3.3) with no significant difference detected between the pre-laying weights in 2000 and 2001 ( $F_{1,232} = 2.005$ ,  $P = 0.158$ ). Table 3.4 shows the similarity in average adult weights during incubation in two consecutive years, with no significant difference detected between the two years ( $F_{1,195} = 3.324$ ,  $P = 0.070$ ). The weight loss experienced by birds during incubation shifts will be explored later in this chapter.

In 2001, adult weights were collected during each phase of provisioning (Figure 3.4). In 2001, a difference in weights was detected between adult weights recorded during the pre-laying season and incubation ( $T_{292} = -2.558$ ,  $P = 0.011$ ). Similarly, in 2001 a significant difference was detected between adult weights recorded during incubation nestling feeding ( $T_{180} = 3.029$ ,  $P = 0.003$ ). However, in 2001, no significant differences were detected for adults weight recorded in the pre-laying season and during nestling feeding ( $T_{274} = 1.575$ ,  $P = 0.116$ ). Furthermore, no significant differences were detected between weight recorded for adults during nestling feeding in 2000, 2001 and 2002 ( $F_{2,566} = 1.855$ ,  $P = 0.157$ ) and is further discussed in context with the range of adult weight measured during food delivery (Chapters 5 & 9). Surprisingly, even between 2000 (a favourable year) and 2002 (a less favourable year)

no significant difference was recorded in the weights of adults during nestling feeding ( $F_{1,496} = 3.431$ ,  $P = 0.065$ ).

**Table 3.3** Mean ( $\pm$  S.D.) adult weights (g) of Little Shearwaters in the pre-laying season in two consecutive years.

	Pre-laying season body mass (g)	
	2000	2001
Mean $\pm$ S.D.	168.3 $\pm$ 12.5	171.3 $\pm$ 12.0
Minimum	137	141
Maximum	194	200
Median	171	172
Mode	171	172
Sample size	40	194

**Table 3.4** The average weights of Little Shearwater adults sampled during the incubation period.

	Adult weights during incubation (g)	
	2001	2002
Average $\pm$ S.D.	175.9 $\pm$ 18.6	171.2 $\pm$ 17.1
Minimum	133	138
Maximum	213	216
Median	176	167
Mode	184	167
Sample size	100	97

#### 3.3.4 Incubation behaviour and adult weights during incubation

During incubation, while one partner remains on land, the other is absent, presumably foraging at sea to replenish body reserves. The duration of these incubation shifts was quantified in 2001 ( $n = 5$ ) and 2002 ( $n = 29$ ). The average duration of the combined incubation shifts was  $7.5 \pm 1.4$  days and ranged from 5 to 11 days (Figure 3.5).

**Figure 3.4** The frequency distributions of adult weights on Beacon Island, during the pre-laying season, incubation and nestling feeding in 2000, 2001 and 2002.

**Figure 3.5** Duration of incubation shifts of Little Shearwaters and absences at sea.



Usually, the duration of an incubation shift was determined by the adult returning from sea, with the incubating adult relieved by its returning partner on 95 % of 40 occasions in 2002 (Figure 3.6). However, an attending bird was observed to leave the egg unattended. The maximum duration recorded for an incubation stint was 11 days. On the following day, this egg was unattended until the next adult returned the following night. Similar behaviour was observed after an incubation stint of 9 days. Consequently, the time an adult spent at sea could exceed the observed length of incubation shifts (Figure 3.5 and Table 3.5).

**Table 3.5** Mean ( $\pm$  S. D.) duration (days) that Little Shearwater adults spent incubating eggs or were absent during late incubation.

	Away from egg	Incubation shift duration		
		Male	Female	Combined
Mean (days)	7.7	7.9	7.2	7.5
Standard deviation	$\pm 1.5$	$\pm 1.4$	$\pm 1.2$	$\pm 1.4$
Minimum	5	5	5	5
Maximum	12	11	9	11
Sample size	25	15	19	35
		One bird could not be sexed		

**Figure 3.6** The incubation behaviour of Little Shearwaters on Beacon Island.

(own file, landscape)

If one compares the incubation shifts of males and females, males appeared to stay with the egg slightly longer than females during late incubation (Figure 3.5, Table 3.5), although no significant difference was detected ( $t_{31} = 1.55$ ,  $P = 0.105$ ).

Hatching was observed to occur when either the male or female partner was present.

Incubation change-overs between adults appeared to be highly co-ordinated and the egg was rarely left unattended (Figure 3.6). The percentage of change-overs recorded in a night seemed to peak periodically at intervals of about 3 - 3 days (Figure 3.7). Here, the barometric pressure experienced during this sample period is also shown, where a drop in pressure corresponds to the passage of a frontal system. Although only a small number of burrows were monitored (8-16), the daily percentage of change-overs between adults during incubation were analysed using cross-correlation analysis in terms of the weather.

Cross correlation frequency analysis suggested that morning wind direction one and two days earlier influenced the number of change-overs occurring in a night, which were recorded in the morning of the following day (Figure 3.8). A significant negative relationship was recorded with evening pressure six days earlier and the number of change-overs. Similarly, a nearly significant relationship was detected with evening pressure differences six and seven days earlier. Morning wind speed five days earlier influenced change-over rates, as did the wind speed in the evening two days later. Such trends may be related to the predictable events associated with the passage of weather systems. Furthermore, the evening flight activity recorded above the island, on the day before, was related to the change-overs observed the next day.

**Figure 3.7** The arrival patterns of adult Little Shearwater during incubation compared to barometric pressure.

**Figure 3.8** Cross-correlation frequencies detected between Little Shearwater incubation change-overs, different weather and activity variables recorded at Beacon Islands in 2002.

In 2001, birds arrived for incubation shifts relatively heavy and departed once their weight had dropped to a certain level, unless relieved by their partner (Figure 3.9). The first weights (recorded on 25 August 2001) do not necessarily depict those at the start of an incubation shift. When possible, the male (M) and female (F) of a pair (identified by burrow code and colour) were monitored. This revealed that male and female weight patterns were very similar during incubation shifts (Figure 3.9).

During 20 incubation shifts, adults averaged a weight loss of  $5.8 \pm 1.4$  g/day (range: 3.5 – 8.5 g/day). For those birds that could be sexed reliably, nine females lost  $5.9 \pm 1.2$  g/day (range: 3.5 – 7.8 g/day) and seven males  $5.5 \pm 1.4$  g/day (range: 3.8 – 8.5 g/day). In 2001, adults were monitored purely to determine weight loss within incubation shifts. In 2002, the focus shifted to determine the duration of incubation shifts with minimal human disturbance and return of maximum depth gauges (MDG).

No significant difference was detected between mean adult weights in 2001 and 2002 (Table 3.6), either on arrival to incubate ( $t_{22} = 0.055$ ,  $P = 0.557$ ), nor upon departure ( $t_{23} = 0.401$ ,  $P = 0.592$ ). The weights were therefore pooled between years and showed that adults arrived significantly heavier than their weight at departure ( $t_{52} = 13.7$ ,  $P = 0.00$ ).

**Figure 3.9** The weights of male and female Little Shearwaters during incubation shifts in 2001.

**Table 3.6** The weights of adult Little Shearwaters at the start and end of incubation shifts in 2001 and 2002.

	Adult body mass (g) during incubation					
	2001		2002		Combined	
	Arrival	Departure	Arrival	Departure	Arrival	Departure
Mean (g)	192.1	155.2	191.7	153.3	191.9	155.0
S.D.	± 9.5	± 9.0	± 13.5	± 7.7	± 11.7	± 8.4
Sample size	13	14	15	12	29	25
Minimum (g)	177	145	155	143	155	143
Maximum (g)	212	173	215	173	215	173

Daily weighing of eggs and adults during incubation, as conducted in 2001, appeared to affect reproductive success. At the 10 burrows monitored during the late phase of the incubation period, nestlings hatched in only six. One egg was predated and another was deserted. One egg was accidentally cracked by a volunteer and another egg by an adult shearwater. Consequently, burrows at which daily weighing of adults occurred during incubation were not included in subsequent analysis nor was the daily weighing of eggs and incubating adults repeated. In 2002, adult handling was minimised to monitor the duration of incubation shifts. Nonetheless, two cases of egg predation occurred when two adults terminated their incubation shift after four and five days at the nest (Figure 3.5). These burrows were not included in the subsequent summation of egg predation.

In 2001, 53 different burrows were monitored using only burrowscopes to determine hatching dates. The periods of time for which each burrow was monitored varied, as some eggs hatched earlier and others were too long to monitor once the burrowscope malfunctioned. A total of 505 burrow inspections occurred during the late phase of



incubation (late August to 15 September) and on 93% of these occasions an incubating adult was present (Figure 3.10). Change-overs between adults were highly co-ordinated, as 95 % of 40 change-overs occurred without egg neglect. If one includes failed breeding attempts, in which one bird left and the other arrived to incubate, 90% of change-overs were co-ordinated.

Unattended eggs were found in 15 (30 %) of the 53 burrows monitored and nine of these failed. Eight eggs were lost when not attended by an adult during a day; one was deserted and monitored for 9 days, with no adult returning. Once one parent had left an egg for a day without the relieving partner arriving, the egg had a 24 % chance of being predated. On Beacon Island, the most likely predators of eggs are Spotless Crakes *Prozana tabuensis*, however Bridled Terns may also kill nestlings to gain nest sites. The eggs were white and typical of burrow-nesting birds. Only once among 143 active burrows documented were two eggs discovered in a burrow. Only one egg was incubated; the second was cold and disappeared in late incubation.

The 54 eggs measured over three seasons had a maximal length of  $49.2 \pm 1.5$  mm and a maximal width of  $35.4 \pm 1.1$  mm, ranging in length from 45.0 to 48.9 mm and in breadth from 33.1 to 35.5 mm. In incubation, egg weights ranged from 25 to 37 g. Eggs were not weighed during laying to avoid undue disturbance and possible termination of the breeding attempt. A value for length x breadth<sup>2</sup>, used as an index for egg volume, averaged 51.8 for 54 eggs, similar to the value of 57 for 15 eggs cited in Warham (1990). The constant for procellariiform birds (Volume x  $0.551 \pm 0.02$ ) was used to calculate an average mass for eggs at laying (Warham 1990) of 34 g (range 30 to 39.5 g).

**Figure 3.10** The percentage of burrows (n = 53) inspected daily that contained an incubating Little Shearwater between late August and mid September 2001.

### 3.3.5 Hatching and guard period

Generally, the offspring began to call within an egg one day before it pecked an air hole in the egg shell. One egg weighed 28 g when pipping (50.1 x 35.5 mm), another 25 g (45.2 x 34.8 mm). The weights of another four pipping eggs were 28, 29, 29 and 30 g and their progress, suggested that these are pre-hatching weights for the Little Shearwater eggs. Once a small hole had been made in the shell by the nestling, hatching occurred slowly. The process from pipping to hatching occurred over intervals of 2, 4, 2 and 2 days respectively. The nestling that hatched over a period of 4 days was still viable, although, some nestlings became stuck to the egg membrane and died if they took too long to hatch. An adult was usually present while the nestling was hatching.

One egg weighed 24 g when pipping with an air hole and the nestling weighed 21 g once hatched. Another weighed 24 g in the egg and 20 g the next day outside the egg. In 2000 and 2001, 15 nestlings were weighed and measured at hatching had a mean weight of  $21 \pm 1.7$  g (range 18-24 g). These nests had not been disturbed prior or during hatching. The hatched nestling was wet, with poor motor control and the head often poorly supported. It often curled up, as if still within the egg, and the eyes were closed. On day two, the nestling was no longer wet, not curled up and the eyes were still half closed, the head was floppy, egg tooth prominent (it persisted for approximately one to two weeks) and, overall, the nestling was more active. On day three, motor skills had improved and the nestling was often able to support its head. The eyes were usually open and overall a more robust image was presented.

The mortality rate of unattended nestlings that had recently hatched was high. After hatching, the nestling lives off its yolk reserves, but weight increased during the day, suggesting that attending adults supplementarily fed the nestling if able to do so. A nestling that hovered below 30 g for several days did not thrive and one in the vicinity of 20 g for three to four days was unlikely to survive (Figure 3.11). Nestlings that were of low weight and subsequently died were much cooler and less active than viable nestlings. Once a nestling had reached an afternoon weight above 30 g, it had a good chance of surviving a missed meal without dropping towards a critical weight (Figure 3.12) and was more likely to survive to fledging.

Upon the researcher's arrival at Beacon Island on 5 September in 2000, some nestlings were already approximately one to two weeks old and hatching continued until 18 September. The ensuing size difference between nestlings prevailed throughout the nestling period. This suggested that hatching is asynchronous in this species and this was investigated in subsequent years.

In 2001, the 39 nestlings monitored hatched over 22 days between 29 August and 19 September (Figure 3.13). Hatching appeared to be spread evenly throughout the whole period, with a slight, but not significant ( $X^2 = 2.18$ ) tendency for nestlings to hatch in the first half of the hatching period. The highest number of nestlings to hatch in a day was four (or 10 %) and this occurred on three days. Overall, 44 % of nestlings hatched within the three days either side of the median of 05 September 2001.

**Figure 3.11** The morning and afternoon weight changes of Little Shearwater nestlings belonging to one of two categories, viable and not viable nestlings, during their first 12 days outside the egg.

**Figure 3.12** Individual nestlings could afford and those that could not afford to be fed for a night.

In 2002, 34 nestlings monitored hatched over 23 days from 28 August until 19 September (Figure 3.13). The greatest number of nestlings to hatch on a single day was 12 %. The median hatch date was 07 September 2002, very similar to the previous year, and 47 % of nestlings hatched within three days of this date. The laying period was calculated to extend from 5 to 27 July based upon an incubation period of 55 days, but may occur slightly earlier, as the recorded incubation period ranges from 52 to 58 days (Glauert 1946). This is in keeping with observations that in late June, at the end of the crayfishing season, no eggs were present in burrows on Beacon Island.

In 2001 and 2002, the attendance of adults was monitored at burrows where a nestling had recently hatched (Figure 3.14). The period monitored in 2001 was shorter than in 2002 and only ran for 13 days, owing to logistical constraints. On the first day that the nestling was outside the egg, an adult was present in all cases in all years. Diurnal attendance at the burrows was high for the first three days of nestling life, although in some instances the nestling remained deserted after the first night (Figure 3.14).

Although, sample sizes were inadequate to test, those adults that left their hatchlings early during the guard period had been incubating for a prolonged period of time and, when handled, expelled faeces that contained green (bile) streaks, rather than the black material indicative of digested prey. In contrast, nestlings attended during the day by adults gained weight, suggesting that supplementary feeding occurred. It is possible that adults depart to forage for a day, during the guard period in order to be able to feed the nestling to ensure its viability.

**Figure 3.13** The hatching dates of 38 Little Shearwater eggs on Beacon Island in 2001 and 34 eggs in 2002 monitored from 28 August to 19 September.



**Figure 3.14** The post-hatching, diurnal attendance of adult Little Shearwaters at the burrow was monitored in relation to nestling age.

Adult absence during the guard period comes at a cost, as two unattended hatchlings were found in bush burrows pecked to death. However, Little Shearwater adults guarding a nestling reacted passively to burrow intrusions from the researcher. Indeed, defence of the nestling is short-lived and often absent, with the adult often scurrying to the depth of the burrow, leaving the nestling exposed to the potential predator.

### 3.3.6 Temporal patterns of adult activity at the colony

Nocturnal counts of the number of birds calling in flight and on the ground fluctuated during late incubation and the transition to nestling feeding (Figure 3.15). The drop in barometric pressure corresponds to the passage of a cold front (Figure 3.15, bottom), also associated with predictable anti-clockwise changes in wind direction in winter. Counts of the number of Little Shearwaters seen flying and the number of call syllables heard in a sample interval, often changed in parallel (Figure 3.16). Unfortunately, the call activity audible at a site could not be used to approximate arrival or departure patterns, since no significant relationship was detected between evening or morning calls and evening or morning flight activity.

**Figure 3.15** The average number of Little Shearwater calls recorded on Beacon Island in the evening and morning from 13 August to 1 October 2002 during nocturnal surveys.

**Figure 3.16** The significant relationships detected using cross correlation frequency (CCF) between different activity parameters measured in this study.

Cross correlation frequency analysis revealed strong relationships between the weather experienced and bird activity (Figure 3.17). Wind direction on the morning of that day affected the number of birds flying in the evening, effectively returning to the colony (Figure 3.17). Furthermore, the wind direction in the evening of the previous day was also of importance in determining the evening flight activity or return of birds from foraging sites. The calls heard in the evening were also related to the morning wind direction experienced on that day (as for flight) and the evening wind direction on the previous day (as for evening flight). Overall, wind direction appeared to be a major factor in predicting activity levels of Little Shearwater at the colony, as this may facilitate travel from distant foraging sites.

Areas of different barometric pressure are the driving force of wind direction and wind speed (Colls and Whitaker 2001). Barometric pressure also influenced arrival and departure behaviour. The evening flight activity was significantly negatively influenced by the evening pressure on that day and positively influenced by the evening pressure three days earlier and morning pressure five days earlier.

Interestingly, the morning flight activity was related to the evening pressure differences between days 4 and 5 earlier and between days 5 and 6 onwards. Such changes in activity are potentially related to the regularity at which weather systems pass across the site, thereby generating similar conditions at cyclic intervals.

**Figure 3.17** The significant relationships detected using cross correlation frequency (CCF) that link nocturnal activity to weather.

## 3.4 Discussion

### 3.4.1 Pre-laying season

Patterns of burrow attendance suggest that the Little Shearwater does not engage in a complete pre-laying exodus, during which both birds leave the island, but such patterns may be obscured by the breeding asynchrony in the colony. It is highly likely that at least the female is absent during a partial exodus.

At Beacon Island, the Little Shearwater laid in July. Two birds were sometimes found in the burrow during the day in May and June. This has also been observed for the Manx Shearwater (Brooke 1990). In 2000, a year of high breeding participation, the larger bird, presumably male, defended the burrow by his presence during the day in June. Male burrow guarding has also been observed for the Manx Shearwater, in which early pairs may be usurped by later breeders, that claim burrows while their owners are on a pre-laying exodus (Brooke 1990). Since weight loss occurs during burrow guarding, presumably there is a limit to the amount of weight a male can lose at this time, as he needs to maintain sufficient body condition to take the first incubation shift, during which he fasts, while the female returns to sea to cover energy costs incurred during egg formation and laying (Brooke 1990).

During the pre-laying season, often more than two birds were encountered at a burrow at night. This may be indicative of competition for limited burrows. However, only 45% of burrows in which two or more adults were identified during the pre-laying season in 2001 saw an egg laid. These observations stem from a year of reduced breeding participation. Alternatively, the visitation by extra birds could present opportunity for extra-pair copulations. DNA samples have been collected to allow

later analysis to determine if social promiscuity results in genetic promiscuity. In New Zealand, Booth *et al.* (2000) twice found a bird in the pre-laying period with an adult with which it did not later share incubation. Extra-pair paternity has been detected in only four procellariiform species (Booth *et al.* 2000), but otherwise genetic monogamy is common in seabirds (Mauck *et al.* 1995) and may be assured by frequent copulations (Hunter *et al.* 1992). In the Procellariiformes, only one offspring can be reared each season, parental care is intensive and shared by both partners, so that any males that manage to fertilise the egg of another care-giving pair, have much to gain (Birkhead and Møller 1992).

#### 3.4.2 Breeding participation

On Beacon Island, overall breeding participation was low in 2001, intermediate in 2002 and high in 2000. In 2000, Little Shearwaters were more likely to use bush burrows to raise nestlings, which were generally located in areas of shallow soil dominated by coral shingles. On Beacon Island, only 28% of burrows with birds present at night during the pre-laying season in 2001 later contained an egg towards the end of the incubation period. Similar rates were measured in New Zealand, where 25 % of Little Shearwater burrows monitored during the pre-laying period later contained an egg (Booth *et al.* 2000). This demonstrates that not all birds returning to a colony will engage in reproduction in a given year.

#### 3.4.3 Mate and site fidelity

In a limited sample, over half of pair bonds remained intact over two successive years and often birds were found at the same location. Nonetheless, some birds were encountered with different partners. However, in no instances was a case of divorce



recorded, with each bird finding a new partner in the following season. In situations where co-ordinated parenting is required, successful pairs should remain stable, as each member can complement the efforts of its partner. In Short-tailed Shearwaters, breeding success increased with the duration of the pair bond, as well as overall experience (Wooller et al. 1989, 1990, Berrow et al. 2000). Similarly, selective advantages were evident for Manx Shearwaters to maintain stable pair bonds (Brooke 1990). This suggests that in shearwaters, individuals would benefit from maintaining, not only their own reproductive potential, but also the reproductive potential of the pair (Brooke 2004).

#### 3.4.4 Egg formation in Little Shearwaters and Wedge-tailed Shearwaters

Egg formation is a large energy and nutrient demand faced by the female alone (Warham 1990). The foraging location accessed by females is of importance, since large eggs produce heavier nestlings with greater survival value (Amundsen et al. 1996, Weidinger 1997). Often higher quality females produce larger eggs (Amundsen et al. 1996). Hence, nestlings that hatch from larger eggs, which are supported by potentially more experienced or higher quality parents have greater survival chances. Heavier nestlings are more likely to overcome the critical post-hatching period, defined by a weight threshold, whereafter they are buffered against disruptions in food for a night (section 3.4.10).

Analysis of egg membranes indicated that female Wedge-tailed Shearwaters within a colony all target similar food during egg formation, whereas, Little Shearwater females displayed no such uniformity. This may be related to their behaviour at sea,

where Little Shearwater adults were not observed to forage in aggregation. Furthermore, it is not known if females engage in a pre-laying exodus which allows them to seek their preferred prey, to generate uniformity. Differences in diet may also result from females visiting different foraging sites, targeting different depths and temporal differences in food availability may be encountered by asynchronously breeding females.

Most foraging by Little Shearwaters appeared at the level of bait-fish, such as Scaly Mackerel *Sardinella lemuru* and potentially small crustaceans (copepods etc.), as indicated by visual dietary analysis. But some Little Shearwaters also have the potential to access this trophic level. Despite, foraging at a trophic level similar to bait-fish, the difference in carbon compositions suggests Little Shearwaters are not feeding exclusively on Scaly Mackerel. This suggests that an interaction with the local purse-seine industry is minimal, at least during egg membrane formation. The purse-seine industry generally targets the inshore areas of the continental shelf, whilst Little Shearwater appeared to feed in offshore waters (Chapter 8).

#### 3.4.5 Incubation shifts

The average duration of incubation shifts (7.5 days; range: 5-11 days) on Beacon Island during late incubation, was similar to that recorded for the larger Little Shearwaters in New Zealand (Booth et al. 2000), where males and females averaged 7.5 and 10 days respectively during early incubation. The duration of incubation shifts usually decreases towards hatching (Warham 1990; Brooke 2004). It is therefore possible that, early in incubation, Little Shearwaters on the Western Australian coast have longer shifts than recorded later in incubation. The West

Australian subspecies is much smaller than the New Zealand subspecies, with a comparatively higher daily weight loss, and might be expected to reach critical weights sooner.

Males and females often have different lengths of incubation shifts (Warham 1990). The incubation shifts of males on Beacon Island were slightly, but not significantly, longer than females. In New Zealand, the duration of incubation shifts did not differ significantly between male and female Little Shearwaters, however it was observed that the males took the first shift after the egg was laid (Booth et al. 2000). Males in some species may take on more of the incubation than females, especially during the early phases, to compensate for the energy expenditure by females during the formation of an egg (Warham 1990; Brooke 2004).

The duration of the incubation shifts recorded for Little Shearwaters are much longer than the 3.5 days for the similarly sized Audubon's Shearwaters (Harris 1969a). Differences in shift duration between species have been attributed to both body size and distance to food supply. Larger birds are able to fast for longer before reaching critical levels (Warham 1990), but the distance to foraging sites and availability of prey may be more important, as they affect the time taken to replenish body condition (Brooke 2004). On the south coast of Western Australia, on Eclipse Island, incubation shifts of two days were recorded for Little Shearwaters (Glauert 1946), suggesting that resources there were more readily available. Similarly, an increase in the duration of incubation shifts was recorded for Audubon's Shearwaters when food was scarce at the same location (Harris 1969a). Thus, in small shearwaters, incubation shift duration can vary between locations and years, consistent with the

suggestion that food availability, and the time taken for adults to replenish weight loss, is the primary factor determining the length of incubation shifts.

A small number of birds departed before the relieving adults returned, suggesting that attending adults had reached a threshold weight, as recorded in other procellariiforms (Chaurand and Weimerskirch 1994a), or that weather conditions were favourable for departure. The relationship of the return and departure of birds from Beacon Island with weather will be examined later. On Beacon Island, a maximum incubation shift of 11 days was recorded; after this, the egg was unattended for a day before the second adult arrived. A similar pattern was observed after an incubation stint of 9 days. This indicates a limit to the time that a bird will fast, while its partner is attempting to regain condition. This implies that any current breeding attempt is secondary to self-preservation.

#### 3.4.6 Weight loss during incubation

Incubating adults cannot forage and, consequently, lose weight. Little Shearwaters arrive at a maximum of 216 g, then rapidly lose weight; thereafter the situation stabilises and a minimal weight of 133 g has been recorded. The minimal weight recorded during incubation was lower than the minimal weights recorded for adults at other times of the annual cycle.

When comparing the weights of adults, which were weighed at the colony during different phases of provisioning in 2001, it became apparent that incubation was most likely the period during which adult weight differed significantly. Birds arrive heavy carrying extra mass to tide over a period of fasting of unknown duration. During

incubation metabolic demands are expected to be low and some dehydration may occur. It is during this phase that it may be possible to measure threshold weights near which birds decide to depart. Conversely, during other phases birds operating near a threshold weight are less likely to be encountered at the island, as they are more likely to be foraging. However, often the threshold weight may not be reached as the attending adult is relieved by its partner returning from sea. The two adults that incubated a nestling for 9 and 11 days lost 45 and 55 g respectively, a drop in 23 - 29 % of the average adult weight at the start of incubation, or 21 - 26 % of the maximum arrival weight.

In New Zealand, female and male Little Shearwaters lost, on average, 5.3 - 5.5 g per day, arriving for incubation around 250 g and departing near 180 g (Booth et al. 2000). This weight loss is equivalent to 2.5 % of arrival body weight. In Western Australia, both males and females daily weight loss during incubation was an average 3 % of the arrival body weight. These values were comparable to the Manx Shearwater, with a loss of 10 g per day or 2.3 % per day (Harris 1955 cited in Warham 1990), and the Audubon's Shearwater, with a daily loss of 5 g or 3.5 %, but a much shorter incubation shift (Harris 1969a).

After an average incubation shift of 7.5 days was recorded where an adult bird lost 3 % of body weight is expected to have lost 22.5 % of its body weight. This compares favourable to the percentage of weight lost by the birds departing after an incubation shift of 9 and 11 days without the arrival of the partner. Over 9 and 11 days one would calculate a loss of 27 to 33 % of adult weight using an average daily

loss of 3 % of body weight. This highlights inherent difference between individuals within a population.

#### 3.4.7 Adult activity and co-ordination of change-overs between partners

Overall, Little Shearwater incubation at Beacon Island was characterised by low egg neglect. Under optimal conditions, parents should co-ordinate their efforts to attend their egg continuously, since predation could terminate their breeding effort and waste resources already allocated. In New Zealand, during 42 % of incubation change-overs, the attending Little Shearwaters left without waiting for the arrival of the relieving adult (Booth et al. 2000). In the current study, about 90 % of change-overs occurred when the next adult relieved the attending adult. This higher level of co-ordination may have been due to predation pressure, because eggs had a 24 % chance of being predated if left alone, presumably by Spotless Crakes or killed by a Bridled Tern to secure a nest site. Furthermore, the data were gathered in the later stages of the incubation period and when eggs may be less tolerant of chilling (Warham 1990). Alternatively, Little Shearwater reproduction in New Zealand was monitored when environmental conditions made it difficult for adults to co-ordinate continuous incubation.

Cross correlation frequency analysis indicated that wind direction one or two days earlier influenced the change-over rate during late incubation and hatching. This suggests that birds used favourable winds to travel between breeding and foraging sites, to increase energy efficiency. Within the colony, incubation change-overs occurred at intervals of about 3 - 4 days, about half the average incubation shift

duration of 7 days recorded for Little Shearwaters in 2002. The frequency of fronts approaching the Western Australian coast is greatest in June and July, with often two large fronts approaching within a week. Whilst in the spring months, including August and September, the frequency tapers off when generally only one front is sufficiently large to influence low latitudes (Meteorology 1998). Laying asynchrony and the weather experienced in early incubation may entrain the 3-4 day peaks in incubation change-overs, despite average incubation shifts lasting 7.5 days. As fronts travel further south in spring, favourable wind directions may arise with the strengthening of high pressure cells. Patterns observed may also reflect changed resource availability, such that adults are able to replenish reserves in a shorter period of time. Hatching is thought to occur when food availability is able to absorb the colonies growing needs (Warham 1990).

Nocturnal activity was monitored during late incubation, hatching and the transition to nestling feeding. Hatching began in the last days of August, signalling the start of a transition phase, during which some pairs still incubated, some brooded and others had already orchestrated a daily food delivery system (Chapter 4). After 7 September, half of the nestlings had hatched. One may assume that the evening flight activity represents the birds returning to the colony. Foremost, the wind direction in the evening of the previous day and the wind direction in the morning of the day influenced the return of birds to the colony. Again, return to the colony is assisted by wind direction foremost, possibly from distant sites given the extended time frame of potentially favourable winds.

Wind direction is a predictable component associated with the passage of weather systems. In contrast, wind speed is often variable and influenced by the differences in barometric pressure between adjacent weather systems (Chapter 1). Most incubation change-overs were defined by the arrival of the relieving adult. This was supported by the strong cross correlation detected between evening flight activity and the number of change-overs detected the next morning. This suggests that Little Shearwater activity may be co-ordinated with predictable components associated with the passage of weather systems, which enable energy efficient travel.

The parameters used to measure nocturnal activity were examined, to ascertain a useful parameter to quickly measure activity of nocturnally arriving colonial seabirds. Flight activity recorded in the evening appeared to be a useful indicator, whilst departure at dawn may have been confounded by *en masse* departure. However, it was not possible to scale colony activity in accordance to the number of calls heard in a night, as call activity was potentially influenced by weather, presence of predators, social facilitation and the structure of the habitat.

Naturally, on windy nights, vocal communication may not be effective and call activity was suppressed, despite birds being present and often, pockets of birds continued to call on a windy night if sheltered by human structures, such as camps. This suggests that the structural composition of the habitat can also influence the behaviour noted. However, by sampling the same areas repeatedly, any effect of the habitat was well controlled.



### 3.4.8 Egg size and payloads

The eggs on Beacon Island were smaller and lighter than those produced by the larger subspecies of Little Shearwater in New Zealand, where egg dimensions were  $35.7 \pm 1.0$  mm (33.3 to 38.5,  $n = 24$ ) by  $54.7 \pm 1.9$  mm (51.4 to 58.0) with a mean laying weight of  $40 \pm 3.9$  g in New Zealand (Booth et al. 2000). In contrast, the calculated average mass at laying was 34 g for Little Shearwaters on Beacon Island. The egg, when laid, was equivalent to 18 - 22 % of the body weight of an adult Little Shearwater. Generally, procellariiform eggs, when laid, represent between 5 and 29 % of female body weight and shearwater nestlings hatch at 9-13 % of adult body weight (see Harris 1959 in Warham 1990). On Beacon Island, a hatched nestling accounted for 11 to 13% of adult Little Shearwater body weight. For Audubon's Shearwater, the egg accounted for 18 % of female body weight and the newly hatched young represented 13 % of the average adult weight (Harris 1959 in Warham 1990). This suggests that payloads experienced by females carrying eggs are greater than would be experienced if having a "live young", although its developmental period may increase the period of encumbrance. Given the effort faced by birds to supply heat to an egg to maintain development within, this seems to be a very ineffective system, especially since the male could deliver food to the "pregnant and encumbered" female sitting in a burrow. The ability for adults to desert the externalised young may be a powerful female risk minimisation strategy. It is possible, that the successful radiation of k-strategist seabirds occurred, owing to the ability to "abort" at will, given that oceanographic conditions can be highly erratic, as demonstrated along the Western Australian coast.

### 3.4.9 Hatching

Little Shearwater nestlings hatched over a two to three week period around 5-7 September each year, with 42 – 47 % of nestlings hatched within three days of this date in 2001 and 2002. It is difficult to estimate laying from hatching in Procellariiformes, as resistance to chilling introduces plasticity in development (Warham 1990). Adults may delay hatching nestlings until favourable weather conditions prevail, as this would increase the chances of crucial food delivery. In 2002, hatching occurred slightly later in the season, and may reflect the less favourable conditions experienced during this year (Chapter 1).

Many species lay at a very predictable time, for instance the Short-tailed Shearwater lays 85 % of eggs within three days (Serventy 1963). This predictability has allowed the reliable harvest of the eggs (Brooke 1990) and nestlings (Brooke 2004), which still occurs in Sooty Shearwaters today (Lyver et al. 1999, Lyver 2000). Similarly, Manx Shearwater laying dates are similar between years, suggesting that female ovulation and possibly laying are entrained by relatively fixed cues (Brooke 1990). At the Western Australian coast, artificial social facilitation was able to move colonies of Crested Terns to different breeding locations, but was unable to alter the onset of breeding activity to an earlier date (Dunlop 1986). However, the population of Common Noddies at Lancelin Island have delayed laying, possibly in accordance to environmental conditions, suggesting that laying cannot occur when resource levels are low, and is delayed if resource levels are not suitable (Nic Dunlop 2005 pers. comm.). Generally, within a colony, it is thought that higher quality or older, more experienced birds are able to lay earlier, while lower quality pairs, possibly younger birds or newly formed pairs, lay later (Brooke 1990; Warham 1990). This has

implications for nestling survival, with earlier laid eggs generally being larger, resulting in larger nestlings (Amundsen et al. 1996) that grow faster (Weidinger 1997).

In New Zealand, a much more protracted laying season of 52 days was recorded for Little Shearwaters, with a distribution that was positively skewed (Booth et al. 2000). A positively skewed laying distribution is widespread in marine birds (Hatch 1990) and may reflect the age distribution of females, with younger, less experienced females laying later in the season (Brooke 1978), whereas pairs with stable bonds lay early (Brooke 1990, Brooke 2004). Furthermore, nestlings that fledge early have a higher survival rate (Perrins 1955 cited in Brooke 1990, Brooke, 1990). Many decisions may already have been made before nestling feeding occurs with the experience of the female and ability of the pair to co-ordinate their efforts influencing nestling survival. This adds to the argument that maintenance of a stable pair bond increases fitness, and therefore that adults should aim to protect the reproductive potential of the pair, rather than selfishly maintain their own body condition (Brooke 2004). Furthermore, it elevates the importance of resource levels encountered during the non-breeding season, as these provide the foundation of each breeding attempt.

A very protracted hatching period of over a month has been recorded for the Little Shearwater on Eclipse Island, off the south coast of Western Australia (Glauert 1946), and also for the Manx Shearwater in high latitudes of the northern hemisphere (Brooke 1990). In comparison, the Little Shearwaters on the central Western Australian coast had a less protracted and more uniform hatching period. In a highly synchronous species, such as the summer breeding Short-tailed Shearwater in

Tasmania, laying spans only 14 days and 85 % of nestlings hatch within three days of a central date (Serventy et al. 1971, Meathral et al. 1993). However, these are birds that are dependent upon seasonally available Antarctic food resources (Klomp and Schultz 2000).

The hatching patterns in a colony may be closely related to the expected duration of the availability of resources that permit breeding and the need to migrate once conditions deteriorate (Brooke 1990). The lower synchronicity of the Western Australian Little Shearwater suggests that, in winter, resources are available for a longer period of time than further south where the Short-tailed Shearwater breeds in summer. Similarly, Wedge-tailed Shearwaters breed in summer along the Western Australian coast, where 74 % of nestlings hatched within three days of a central date (Chapter 7). This may indicate that, along the Western Australian coast, summer conditions that facilitate reproductive activity are less stable than in winter. This may be why Little Shearwaters breed in winter, in addition to reducing competition for limited space on islands.

Little Shearwaters were not as asynchronous as the Christmas Island Shearwater and Audubon's Shearwater, which lay and hatch nestlings all year around (Harris 1969a). More tropical locations may be more stable temporally than conditions off the central Western Australian coast, where oceanographic conditions are influenced by SOI conditions and fluctuate greatly within and between years. Western Australian locations lack stable and predictable upwellings, so that hatching asynchrony within a colony may spread resource utilisation over longer, and thereby reduce competition. In tropical areas, characterised by sustained low productivity, there is little to gain

from more synchronous hatching, which results in peak utilisation of resources. This contrasts with species whose reproductive efforts depend on highly abundant resources predictably available in a given season and which have much to gain from matching peaks in food requirements with food availability despite competition.

#### 3.4.10 Post-hatching adult attendance

The constant attendance of nestlings during their first three days of life suggests that this is a crucial period. Indeed, the mortality rate of unattended, recently hatched nestlings was high. Defence of the nestling by the adult was short-lived and often absent, the adult often scurrying deep into the burrow, leaving the nestling exposed to any potential predator. This implies that survival of the nestling is secondary to that of the adult, although most predators are deterred by the presence of the adult.

Shortly after hatching, the nestling may not be able to thermoregulate, has poor motor skills and may benefit from heat and supplementary food provided by the attending adult, in order to accelerate its passage into a viable nestling. Since nestlings gained weight when an adult was present during the day, they are likely to be supplementarily fed by the attending adult, rather than living solely upon the yolk.

Interruptions of the guard period may reflect an inability by the adult to supplementarily feed a nestling. If, prior to hatching, an attending parent had been present for a long incubation shift, then no undigested food should be present within its digestive tract to feed to the nestling. It appeared as if the relieving partner did not arrive with a full stomach during the first night after hatching, then the attending parent departed to source food, leaving the nestling unattended. Absences during the guard period came at a cost, however, with two unattended nestlings found pecked to

death in a bush burrow. At this stage, investment in the nestling is large and risks are high, which suggest that the adults' behaviour has large benefits. The rapid return of the adult (i.e. after one day at sea) suggests that its primary focus was the provision of fresh food to the nestling rather than self-maintenance, which generally occurs during longer absences (Chapter 4).

Little Shearwater hatchlings appeared less likely to perish once an afternoon weight over 30 g had been reached. Often egg size is related to female age and possibly quality. Furthermore, hatching success and often over all growth rate was related to egg size (Amundsen et al. 1996). The importance of female foraging during egg formation is highlighted, since larger eggs hatched heavier nestling Antarctic Petrels *Thalassoica antarctica* (Amundsen et al. 1996) and Cape Petrels (Weidinger 1997). This indicates that foraging success of females has great influence on nestling survival. Heat loss increases proportionately as body size decreases so that small individuals need to increase metabolic rates earlier than larger ones to offset potential drops in body temperature. Smaller individuals also have a higher critical temperature and must grow, or perish, as it is risky to remain small for too long (Peters 1993). Shearwater nestlings have a thick layer of down that may minimise heat loss to the environment during their slow growth. The amount of food delivered by adults and the pattern of its delivery will be examined in Chapter 4 and ramifications of this input system for nestling growth will be examined in Chapter 5.

## **4 Chapter 4: Little Shearwater parental provisioning during nestling feeding**

### **4.1 Introduction**

This chapter explores how often and how much Little Shearwater nestlings are fed and investigates the mechanism by which adult shearwaters determine temporal patterns of provisioning whilst feeding nestlings at a location characterised by instability of oceanic conditions (Chapter 1). Patterns of provisioning adopted earlier in the breeding cycle are discussed in Chapter 3, whilst this chapter continues with pattern of provisioning observed from the end of the guard period to fledging, during which time one or both of the parents is thought to return at night to feed the nestlings (Warham 1990). Overall, the pattern of parental care allocated may be dictated by prevailing weather patterns and availability of oceanographic resources. The amount of food consumed by the nestling and the rate at which it is supplied define the input system, which supports nestling development (Chapter 5). In later chapters this information will contribute to the ongoing debate on the function of nestling obesity.

Little Shearwaters were expected to feed their nestling regular, small meals. Frequent weighing is often used to determine the amount of food delivered (Ricklefs 1984b, Ricklefs et al. 1985, Hamer and Hill 1993, Hamer 1994, Bolton 1995, Hamer and Hill 1997, Hamer and Thompson 1997). In this procedure, nestlings are weighed at set intervals during the night, but this did not affect the meal sizes delivered to nestlings, nor their rate of delivery, in Cory's Shearwaters (Hamer and Hill 1993), Little

Shearwaters (Hamer 1994) and Short-tailed Shearwaters (Schultz and Klomp 2000b, a).

Generally, frequent weighing focuses on an intense, short study period. It can also determine how often and when nestlings are fed but data may be biased towards the conditions encountered during a short period (Weimerskirch 1998; Schultz and Klomp 2000a). It is known that Little Shearwaters depart *en masse* at dawn, but little is known about their temporal pattern of arrival within a night. Consequently, the nightly arrival pattern of adults was also investigated using data generated during frequent weighing. In this study, other less labour intensive methods were also used to examine long term temporal patterns of provisioning and to comment upon the application of data generated using frequent weighing.

Little Shearwaters have been documented to use a co-ordinated, bimodal foraging strategy in New Zealand (Booth et al. 2000b), although it is not known how it is co-ordinated. It was not known if the Little Shearwaters breeding on the Western Australian coast also adopt a bimodal foraging strategy. The temporal patterns of provisioning and adult attendance were observed during nestling feeding and compared with prevailing weather conditions.

Adults obtain food for their dependent nestling and themselves at sea, resulting in an energy transfer from the foraging site to a central breeding site. Patterns of food delivery to the nestling differ between species of shearwater and may reflect different life-history strategies (Warham 1996). However, within a species, provisioning patterns may also vary between locations and years. The Little Shearwater has been



studied at other locations (Glauert 1946, Hamer 1994, Booth et al. 2000, Booth et al. 2000b, Priddel et al. 2003) allowing comparisons between different breeding sites. Along the Western Australian coast, inter-annual fluctuations in environmental conditions occur (Chapter 2) and provisioning in the Little Shearwater was examined in what is known to have been a favourable (2000) and less favourable (2002) year for reproduction for other shearwater and seabirds along this coast (Dunlop and Wooller 1990, Wooller et al. 1991, Integrated Shearwater Monitoring Program 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, 2003, 2006). The mechanism by which adults adjust provisioning in accordance with such annual differences in conditions is explored and will contribute towards the discussion of life history strategy adopted by a long-lived species in an unstable environment.

## **4.2 Methods**

### **4.2.1 Frequent weighing**

A representative group of nestlings were weighed at 4 h intervals and in the same order. Since Little Shearwater adults were present until dawn, attending adults were also weighed and identified throughout frequent weighing. Frequent weighing of nestlings was conducted over 10 consecutive nights in 2000, and over a period of three consecutive nights in both 2001 and 2002. In 2000, 21 burrows were monitored from 23 September until 03 October, 24 burrows from 01 to 04 October in 2001 and 23 burrows from 02 to 05 October in 2002.

### **4.2.2 Adult patterns of provisioning during nestling feeding**

In Procellariiformes, parental provisioning requires the efforts of two partners. During the frequent weighing period in 2000, the presence of adults was noted

throughout the night in most burrows. This has been recorded in other studies of Little Shearwaters (Glauert 1946, Priddel et al. 2003). Subsequently, adults were banded, measured and weighed over several nights, delaying the start of frequent weighing until a round could be completed in 20-30 minutes. As a result, both the nestlings and attending adult could be weighed and identified during frequent weighing. Subsequently, the start of frequent weighing was delayed for a night, to allow the banding of adults. Thereafter, the weight and identity of each adult was noted during the 10-night frequent weighing period in 2000. This gave rise to an 11-night snap-shot of adult attendance and their weights at 21 burrows in 2000.

For the Little Shearwater, the pattern of adult attendance recorded in 2000 over a 10 day period during frequent weighing was analysed to exclude in being a random. A Monte Carlo randomisation method (Manly 1991) was used to test if the number of joint presences and joint absences observed in the data was the result of random presence and absence by the two birds of each pair. Using a Fortran computer program, the number of nightly visits of each bird to its burrow were allocated at random to the eleven days of the study; i.e. the attendance of a bird that visited for seven nights was represented by seven nights allocated at random out of the eleven. The number of nights on which both birds were present and on which both birds were absent was then determined across the 21 burrows. This procedure was replicated 10000 times to generate an empirical cumulative density function for the number of joint presences and absences.

The temporal attendance patterns of marked individuals were also noted during frequent weighing. Since adult Little Shearwaters stay at or near the nest until dawn,

they were relatively easy to identify. Throughout the analysis the following terminology will be used. “Change-overs” were defined as the return of one partner, absent for a prolonged period (as in incubation) only if it was scored within the night (not in the following morning as in incubation), which may or may not have resulted in an overlap with the attending partner, resulting in the presence of “two adults”. The term “departure” implied that a bird left and did not return at least for a night or more. Only a subset of these departed adults were absent for longer than one night; these were labelled as “birds not returning” and were assumed to have departed on a foraging trip of a longer duration. Such direct methods were not suitable for species that only visit the nest briefly, such as the Wedge-tailed Shearwater.

For the Little Shearwater, the pattern of adult attendance recorded in 2000 over a 10 day period was analysed for relationships with weather using cross correlation frequency performed by SPSS Statistical Package for Windows. Weather variables tested included the morning and evening pressure, morning and evening wind direction and speed. The pressure differences over 24 h were calculated by subtracting the previous days pressure value from that for the day concerned, separately for the morning and evening. This process used a drop in pressure as an indication of the passage of a front.

When living on Beacon Island, it became apparent that adults arrived at different times of the night, ranging from dusk to well after midnight. The timing of adult arrival in three 4 h periods of darkness was estimated using nestling weights during frequent weighing in 2000. Weight changes were recorded in nestlings between 17:30 - 21:30 h, 21:30 h – 01:30 h and 01:30 h – 05:30 h. The presence of Little

Shearwater adults during frequent weighing had also been noted, but positive weight differences during the night were used as a measure of the presence of an adult. It was assumed that Little Shearwaters generally fed their nestling soon after arriving at the colony. The weight changes of nestling were used to estimate adult arrival. This method allowed comparison to Wedge-tailed Shearwaters, which do not remain at the nest for prolonged periods of time.

#### 4.2.3 Adult activity during nestling feeding

A longer term index of parental provision was thought and nestlings were weighed twice daily. The percentage of nestlings fed each night was determined using 12 h weight changes (Booth et al. 2002), with a 5 g weight difference over 12 h chosen to indicate a feed in Little Shearwaters. In 2000, morning and afternoon weights were obtained from 07 September to 22 October, 27 - 28 October, 04 - 05 November and 10 - 23 November. In 2002, they were taken from 07 - 22 September, 28 September to 06 October and 12 October to 18 November. For 2000 and 2002, the average morning and afternoon weights of nestlings were plotted over time to compare different years.

### 4.3 Results

#### 4.3.1 Adult weights during nestling feeding

During nestling feeding, no significant difference was detected between the weights recorded for adults in the three years ( $F_{2,566} = 1.855$ ,  $P = 0.157$ ). The weights of adults encountered at night during the nestling feeding phase ranged from 137 to 217 g (Table 4.1). This range illustrates the dynamic nature of adult weights during

nestling feeding, when adults arrived carrying food and departed lighter after feeding. Note that in 2001, hardly any departing parents (Figure 4.4), in the lower weight range, were sampled and a higher average weight was recorded (Table 4.1). A subset of adults, weighed during frequent weighing in 2000, is considered later in the chapter in the context of food delivery and payloads.

The average weight recorded for all adults encountered during the study period, including the pre-laying season and incubation, as well as nestling feeding, was  $169.7 \pm 14.5$  g with a range of 133 to 217 g ( $n = 1000$ ) with a median of 169 g and a mode of 158 g (please consult Table 3.3 and 3.4 for adult weights during the pre-laying season and incubation).

**Table 4.1** Mean weights ( $\pm$  S.D.) of adults encountered at night during the nestling feeding period in three different years. The adults weighed included those that had fed their young and those that still carried food.

	Body Mass (g)			
	2000	During nestling feeding		Combined
	2000	2001	2002	Combined
Mean $\pm$ S.D.	$168.5 \pm 14.2$	$193.9 \pm 10.7$	$165.3 \pm 15.1$	$168.0 \pm 14.0$
Minimum	141	152	137	137
Maximum	217	204	217	217
Median	167	167	163.5	167
Mode	158	158	150	158
Sample size	416	71	82	569

**Figure 4.1** The frequency distribution of weight difference (uncorrected meal sizes) measured for Little Shearwater nestlings on Beacon Island in 2000, 2001 and 2002.

### 4.3.2 Meal size

The positive weight increases over 4 h intervals recorded for nestlings in 2000, 2001 and 2002 are shown in Figure 4.1, prior to correction for inherent weight loss. In each year, inherent weight loss may be affected by a different set of variables. In 2000, log weight loss was influenced by the burrow of origin ( $F_{20,279} = 2.26$ ,  $P = 0.002$ ), and also the log of the previous weight ( $F_{1,279} = 20.57$ ,  $P = 0.000$ ). In 2001, log weight loss was influenced by the log of the previous weight of the nestling ( $F_{1,54} = 9.05$ ,  $P = 0.004$ ), but no significant relationship was picked up in 2002.

A regression equation was calculated for each year. In 2000, a strong relationship ( $r = 0.84$ ) was detected between meal size and corrected meal size when relevant factors were incorporated (Figure 4.2 top) and a corrected mean meal size of 35.0 g was then determined (Table 4.2). In 2001, when a strong relationship existed ( $r = 0.80$ ) between meal size and corrected meal size (Figure 4.3 middle), a corrected mean meal size of 25.2g was determined (Table 4.2). In 2002, a strong relationship ( $r = 0.751$ ) between meal size and corrected meal size also existed (Figure 4.3 bottom), allowing a corrected mean meal size of 32.3 g to be calculated (Table 4.2).

A strong relationship was detected between the corrected meal size and the uncorrected meal size in all years (Figure 4.2). This made it possible to use the total overnight food consumed and weight changes over a 24 h (NET) period to calculate meal sizes required for zero growth (Figure 4.3 and Table 4.2). In all years, Little Shearwater nestlings received sufficient food to maintain their weight.

**Table 4.2** The mean ( $\pm$  S.D.) weight differences, corrected meal sizes and the total amount of food needed for zero weight gain over 24 h (maintenance meal) by nestlings. The number of meals delivered per night is also given for Little Shearwater nestlings on Beacon Island in early October in 2000, 2001 and 2002.

	Provisioning		
	2000	2001	2002
Number of meals per night $\pm$ S.D.	1.1 $\pm$ 0.04	0.86 $\pm$ 0.07	1.1 $\pm$ 0.07
Weight difference (g) $\pm$ S.D.	31.6 $\pm$ 0.8	22.5 $\pm$ 12.7	24.4 $\pm$ 10.7
Maximum weight difference (g)	79.5	52.0	62.5
Corrected Meal size (g) $\pm$ S.D.	35.0 $\pm$ 1.1	25.2 $\pm$ 2.1	32.3 $\pm$ 1.9
Maximum corrected meal size (g)	101.7	64.7	68.0
Maintenance meal size (g) $\pm$ S.D.	32.2 $\pm$ 0.76	24.0 $\pm$ 1.76	29.6 $\pm$ 1.83

A strong relationship was detected between the corrected meal size and the uncorrected meal size in all years (Figure 4.2). This made it possible to use the total overnight food consumed and weight changes over a 24 h (NET) period to calculate meal sizes required for zero growth (Figure 4.3 and Table 4.2). In all years, Little Shearwater nestlings received sufficient food to maintain their weight.

Food delivery rate and frequency appeared to differ between years. The number of meals received per night suggested that, in 2001, the provisioning rate was lower than in 2000 and 2002 (Table 4.2). Furthermore, in 2001, fewer and smaller meals (Table 4.1) were delivered to nestlings compared to other years. Similarly in 2001 only 75 % of nestlings received one or more meals during 24 h period compared to 91 % in 2000 and 90 % in 2002 (Table 4.3) during relatively short sampling intervals.



**Figure 4.2** A strong relationship exists between the corrected meal sizes calculated using a regression equation and the weight difference measured in 2000, 2001 and 2002.

**Figure 4.3** The intercept of the horizontal line with the y-axis gives the overnight food consumed to maintain zero weight gain over 24 h in Little Shearwater nestlings in 2000, 2001 and 2002.

**Table 4.3** The frequency (percent) of the number feeds received by a Little Shearwater nestling during a 24 h period.

Number of meals per night	Frequency (%)		
	2000	2001	2002
0	19 (9)	18 (25)	7 (10)
1	154 (73)	46 (64)	48 (70)
2	35 (17)	8 (11)	14 (20)
3	3 (1)	0	0
Total number of intervals monitored	211	72	69
Number of sample nights	10	3	3

#### 4.3.3 Total overnight food consumed during growth

The total food consumed overnight by nestlings in a favourable year (Figure 4.4 top) followed a pattern typical for procellariiform nestling weights over time. Initially, the total food consumed overnight increased with time, then decreased before fledging as weight loss occurred. Note that this figure is categorical and does not display the gaps in monitoring, which occurred in 2000 at peak mass from 23 –26 October, 28 October to 03 November and 05 – 09 November. Similarly, in 2002, a break in monitoring occurred from 22 September to 27 September and from 6 to 11 October. An overview of the total food consumption over time is given in Table 4.4 where consumption has been summarised in 10 blocks. In 2002, the total overnight food consumed by nestlings was highly erratic (Figure 4.4 bottom), but nevertheless showed a less defined increase with age until the pre-fledging weight loss period, a trend also apparent in Table 4.4. Meal sizes were smaller and nestling weights were lower in 2002 than in 2000 (Figure 4.4, Table 4.4). Although, Little Shearwater nestlings consumed smaller meals (Table 4.4) and were fed less often (Figure 4.5) during the pre-fledging weight loss period, most nestlings were not deserted completely (Figure 4.6). However, some nestlings were not fed for up to a week before fledging.

**Figure 4.4** The mean ( $\pm$  S.D.) total food (g) consumed overnight by Little Shearwater nestlings on Beacon Island in 2000 and 2002.

**Table 4.4** The mean mass ( $\pm$  S.D.) of nestlings, mean weight difference (uncorrected meal size) and overall nightly food received by nestlings on Beacon Island in 2000 and 2002 during consecutive ten-day blocks.

**Figure 4.5** The percentage of Little Shearwater nestlings fed before fledging; data for 2000 and 2002 have been combined.

**Figure 4.6** The pre-fledging feeding history of 25 Little Shearwater nestlings; data from 2001 and 2002 have been combined.

#### 4.3.4 Bimodal foraging and the co-ordination of parental care

Adult attendance at burrows was documented for 11 days in 2000 (Figure 4.7). In general, the same adult fed a nestling nearly every night for several consecutive nights, resulting in regular food delivery; at such times, the other adult was not recorded at or near the burrow. Occasionally, the nestling remained unfed and the adult attending daily was absent for a night, whereafter it generally continued its daily attendance.

Overall, the change-overs between attending adults appeared to be highly co-ordinated. Although difficult to score, approximately 70-83 % of change-overs between adults occurred without the nestling remaining unfed. During successful change-overs where continuous food delivery resulted, the adult attending daily was present on one night and the other adult was recorded the following night.

Alternatively, both adults were recorded at the burrow together in the same night. Generally, an overlap of adults signalled the start of the returning adult's period of daily provisioning, whilst the adult previously attending daily was not recorded at the burrow for a while. However, in some instances the pattern was less distinct suggesting that some pairs are better than others in co-ordinating food delivery.



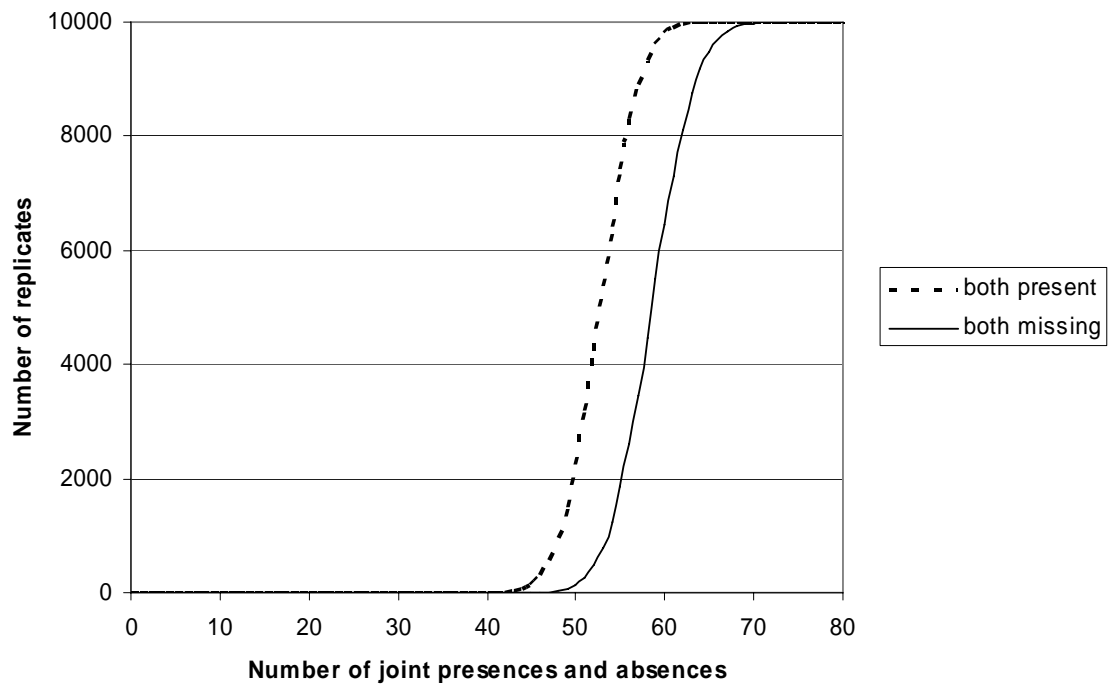
**Figure 4.7** Adult attendance patterns at the burrow from 22 September to 02 October 2000. It should be noted that not all birds on short trips returned daily.

A Monte Carlo randomization method (Manly 1991) indicated that the number of joint presences and joint absences observed in the data was not the result of random presence and absence by the two birds of each pair. This procedure was replicated 10000 times to generate an empirical cumulative density function for the number of joint presences and absences (Figure 4.8). In the original data both birds were present together on 21 occasions and both birds were absent on 21 occasions out of the 231 burrow nights observed. The cumulative values for 21 joint presences and 21 joint absences out of the 1000 replicates was zero in each case, indicating that the empirical probability of a result of 21 or less was smaller than 0.001.

Using an 11-day sequence of adult patterns of attendance in 2000 (Figure 4.9), temporal patterns included complete sequences: from the return of one bird to relieve its attending partner, to the prolonged departure of a bird relieved by its returning partner and its subsequent return. In 2000, periods when one parent attended to a nestling daily lasted, on average,  $5.9 \pm 1.1$  days (Table 4.5) and prolonged absences lasted on average  $5.2 \pm 1.3$  days. The absences showed a bimodal pattern (Figure 4.9), indicative of a dual bimodal foraging strategy.

**Table 4.5** The duration of periods (in days) during which a parent attended the nestling daily and the duration of the long absences birds were away from the colony.

	Duration of continuous daily attendance shift	Duration of prolonged absence from colony
Average $\pm$ S.D.	$5.9 \pm 1.1$	$5.3 \pm 1.3$
Sample size	25	24
Minimum	3	2
Maximum	7	8
Total single trips recorded	123	
Number of days nestling was not attended	4	



**Figure 4.8** The pattern of empirical cumulative density functions of joint presences and joint absences generated by a Monte Carlo simulation suggests that the adult attendance observed in this study was unlikely to have been produced by random attendance.

**Figure 4.9** Adult attendance patterns at the burrow from 22 September to 12 October 2000 showing a bimodal pattern.

A high number of change-overs appeared to coincide with the passage of a front during the nights of 25/26 September to 27/28 September 2000 (Figure 4.7). On 27 and 28 September 2000 it rained on Beacon Island, while light rains occurred on 29 September, signalling the passage of a front. Fronts are associated with a drop in barometric pressure and an anticlockwise swing in the wind direction. When the front hits north-westerly ( $315^{\circ}$ ) winds persist.

Cross correlation analysis (Figure 4.10) suggests that adult behaviour may be influenced by weather variables, although it is difficult to isolate a definite, singular parameter which may be of importance to the birds. Change-overs were defined as the return of the absent partner, and included cases where it did, and did not, overlap with the bird engaged in daily attendance. It gives some indication of the weather needed to support the return of an adult from a foraging location. The number of change-overs between adults was significantly influenced by the wind direction experienced in the evening of the day that the birds arrived and significantly related to the wind direction two days later. A one night overlap in adults was related to the morning wind direction experienced on the day (Figure 4.10 titled “with two adults”), (see Figure 4.7 and 4.11). It seems that the nestling gained more weight during times, when two adults were present and evidently lost weight when no adult was present in a night (Figure 4.11). The departure of adults from Beacon Island and their absence for at least a night was related to the barometric pressure experienced in the morning two days earlier (Figure 4.10 titled “with departure”). However, 27 % of these birds returned to the colony to continue daily provisioning after being absent.

**Figure 4.10** The cross correlation frequencies (CCF) detected between different weather variables and the number of change-overs, two adults or the departure of an adult (without the arrival of its partner) was recorded at 22 burrows over 11 nights in 2000.

**Figure 4.11** The decreases in the post-feeding weights of adults attending to their nestling daily were recorded.

#### 4.3.5 Nightly fluctuation of adult weights with food delivery

Adult weights were monitored for 11 nights during nestling feeding from 22 September to 02 October 2000 (Figure 4.12). At the time, when the lowest adult weight was recorded, the nestling had gained weight, indicating that the post-feeding weight was recorded for each adult during each night. The post-feeding weights of a given adult were significantly greater at the start of a period of daily provisioning than at its end (Table 4.6) (assuming unequal variances,  $t_{41,6} = -13.0$ ,  $P = 0.00$ , since Levenes test:  $F_{67} = 14.2$ ,  $P = 0.00$ ). Over a period of daily attendance, post-feeding weights of parents displayed an average daily decrease of 3 % of adult weight (Table 4.6).

**Table 4.6.** The mean post-feeding weight of an adult at the start and the end of a period when it attended the nestling daily. These values include many instances when both adults were present to feed a nestling and four occasions when the adult on daily provisioning missed one night of feeding and stayed at sea.

	Post-feeding weight at the start of daily provisioning (g)	Post-feeding weight at the end of daily provisioning (g)	Mean daily weight loss (g/day)	Average duration of monitoring for weight loss (days)
Average $\pm$ S.D.	185.2 $\pm$ 11.3	154.2 $\pm$ 7.0	5.0 $\pm$ 2.5	5.1 $\pm$ 1.3
Minimum	163	142	2.0	2
Maximum	201	171	14.7	7
Sample size	29	40	35	34



**Figure 4.12** The percentage of Little Shearwater nestlings fed at different times at night during frequent weighing in 2000, 2001 and 2002.

Adults appeared to deliver a similar mass to the nestling throughout a period of daily attendance, despite slightly decreasing in post-feeding mass over time (Figure 4.11). The mass delivered by an adult during a period of daily attendance does appear to drop slightly and may warrant further investigation. Large weight differences in the nestling were generally recorded when both adults attended their nestling during the same night. Occasionally, a nestling recorded a negative weight difference, indicating that it had not been fed, associated with the absence of any adult at the burrow. Indeed, all adult visits were associated with a mass increase in the nestling, which became an underlying assumption in this study.

#### 4.3.6 Nightly patterns of adult arrival and nestling feeding

In 2000, when monitoring was longest, most Little Shearwater nestlings were fed before 21:30 h (Figure 4.12). Patterns of weight gain were also documented over three day periods in 2001 and 2002, when once again most nestlings were fed early in the night (Figure 4.12). However, more nestlings may have been fed later in the night in 2001 and 2002 (Table 4.7), when adults may have arrived later than in the favourable year 2000. Occasionally, nestlings were fed twice in a night, either by the same or a second adult. In 2000, of the total number of feeds recorded, 11 % were second feeds consumed by a nestling within the same night and 91 % of these second feeds were received in the 21:30 – 01:30 h period. Despite, the smaller sample periods than in 2000, a similar proportion of second feeds were recorded in 2001 (9%), and 2002 (11 %).

**Table 4.7** The percentage of nestlings that were fed] and percentage of first meals delivered in each time slot: dusk to 21:30 h, 21:30 h to 01:30 h, 01:30 h to 05:30 h. Naturally, all meals registered in the first sampling interval at 21:30 h were first meals. In 2000, 21 burrows were surveyed for 10 nights; 24 burrows were visited in 2001 and 23 burrows in 2002 for three nights in each year.

	21:30	1:30	5:30		
	Percent fed	Percent fed	Percent first meals	Percent fed	Percent first meals
2000	75.6	21.4	54.3	2.8	66.7
2001	52.2	36.2	72.0	11.6	100
2002	52.9	36.0	82.0	11.4	100

12 h weight differences were used to estimate the percentage of nestlings fed by adults in 2000, 2001 and 2002. This percentage fluctuated both within a year and between years (Figure 4.13). Provisioning rates appeared to be consistently highest in 2000. In the other two years, when data were less continuous, provisioning nonetheless appeared both less uniform and reduced. In 2000, a distinct reduction in provisioning levels occurred towards fledging. The use of 12 h weight differences may have missed instances of nestlings being fed small meals. During the brief period of frequent weighing, 91 % of nestlings in 2000 (n = 21), 75 % in 2001 (n = 24), and 90 % in 2002 (n = 23) received at least one meal (Chapter 6). This is greater than the percentage of nestlings fed over the same period using morning and afternoon weights, with an average  $88 \pm 7$  % (range: 70-96) of 60 nestlings fed in the ten nights monitored in 2000. In 2001, on average,  $70 \pm 7$  % (range: 65-77) of 35 nestlings were fed nightly compared to  $86 \pm 18$  % (range: 65-96) of 23 nestlings in 2002. In 2000 and 2001, a smaller sub sample was used for the frequent weighing, whereas in 2002 all nestlings were used for frequent weighing,

**Figure 4.13** The percentage of Little Shearwater nestlings fed on Beacon Island from 8 September to 22 November in 2000, 2001 and 2002.

allowing for a direct comparison with 12 h weight differences. Overall, the average percentage of all nestlings estimated to have been fed during the frequent weighing period using 12 h weight differences was slightly lower than the values obtained using 4 h weight differences.

The difference between morning and afternoon weight has been used by others to estimate the percentage of nestlings fed (Booth et al. 2000). Under the windy conditions at the Houtman Abrolhos Islands, a 5 g difference or greater was registered as a feed. This approach may under-represent feeding frequency at times when adults struggle to gather large meals for their nestlings. A direct comparison of the percentage of nestlings fed, suggests that the 12 h weight differences, with a 5 g cut off, underestimated feeding frequency by approximately 5 %, probably because small meals were missed, they had already metabolised by the morning. However, the 12 h weight difference, gave a picture of fluctuations in provisioning over time, since the less intensive protocol could be sustained for much longer. The 12 h intervals were also more sensitive than using 24 h weights for which meals often just offset maintenance needs.

#### 4.3.7 Real-time patterns of weight gain in nestlings

Nestling weights followed a typical pattern of nestling weight gain (Figure 4.14), with a gradual increase to a peak mass, then weight loss before fledging. Figure 4.15 shows the number of nestlings monitored in 2000 and 2002 to produce Figure 4.14. The differences in sample size between the years reflects the ease of locating accessible nestlings in a favourable year, such as 2000, when reproductive participation is high, compared to a less favourable years 2002. In 2000, just prior to fledging the apparent increase in average weights probably stems from the dwindling

**Figure 4.14** The real time average weights of Little Shearwater nestlings recorded in the morning and afternoon in 2000 and 2002.

**Figure 4.15** The number of nestlings monitored to produce average morning and afternoon weights in 2000 and 2002 from early September to late November.

sample size. This pattern was not noted when weighing individual birds and thus reflects hatching asynchrony, resulting in the nestlings monitored each day being of different ages and sizes. Regular fluctuations in weight are apparent between afternoon and morning weights, indicating a similar pattern of influx of food to the colony in both years.

## **4.4 Discussion**

### **4.4.1 Adult weights during nestling feeding in different years**

No significant difference was detected between the adult weights recorded during the nestling feeding between the three years. In each year and during each phase of reproduction, adult weights fluctuated. This is consistent with adults meeting immediate demands of reproduction, whilst foremost maintaining a threshold body condition (Takahashi et al. 1999, Takahashi et al. 1999b). During brooding, weight loss originates from a lack of opportunity to feed. However, Little Shearwaters limited the time they spent fasting during incubation, presumably based on a threshold body condition, after which they departed to sea to forage (Chapter 3). During nestling feeding, adult weight loss arose from energy demands associated with orchestrating a near daily pattern of food delivery to the nestling from potentially distant and mobile foraging sites. A similar range in weights was noted during the 2000 pre-laying season when birds were possibly guarding burrows and during the incubation period (Chapter 3). These natural fluctuations in adult weights associated with breeding activities, illustrate the difficulty faced in attempting to define an average adult weight.



Average adult weight is greatly affected by sampling effort. For example, a larger ratio of pre-feeding to post-feeding birds sampled may account for the greater average adult weights recorded in 2001 than in other years (Table 6.1). The fluctuations in weights, experienced by individuals as they meet reproductive loads, also affect the ability of average weight to be used as an absolute index of adult body condition. Minimal weights may give a better indication of the threshold body condition at which an individual withholds further provisioning and needs to replenish its body condition. Whilst, a maximal weight at which the bird returns to the colony, in the case of a bimodal foraging strategy, gives an indication of its ability to sustain the next period of intensive care. Adult shearwaters are thought to protect their own body condition, and possibly that of their partner, in order to maintain the reproductive potential of the pair, particularly when breeding success increases with the duration of the pair bond (Brooke 2004).

#### 4.4.2 Frequent weighing and the nestling

Environmental conditions suggest that 2000 was a favourable year for seabird reproduction on the west coast (Chapter 1). This was also true for Little Shearwater reproduction, as breeding participation was higher in 2000 compared to 2001 and 2002 (Chapter 3). As a result, the quality of pairs participating was likely to be highly variable and it is likely that this accounts for the difference in nestling weight loss noted between burrows in 2000. It may also explain why food delivery by some pairs was highly co-ordinated, whereas other pairs did not manage to orchestrate a regular food delivery to the nestling in 2000 (Figure 4.7). Unlike 2000, when burrow of origin influenced weight loss, in 2001 and 2002, no difference in weight loss was

detected between burrows. This may have been due to the shorter duration of the frequent weighing period. Alternatively, it may suggest that in less favourable years, when breeding participation is reduced, only individuals of higher quality are able to participate in nestling rearing and competition is reduced.

In 2002, weight loss was not influenced by past feeding events. This suggests that Little Shearwater nestlings may set their metabolic rate in accordance with poor feeding history. In 2000, when conditions were better, the previous weight of the nestling was of importance to weight loss. Therefore, both nestling and parents may be affected by the prevailing conditions.

In 2000 and 2002, body size also affected weight loss. In 2001, body size was not important, suggesting that a more evenly aged group of nestlings had been chosen. Otherwise, it might be expected that a smaller body size, with its greater surface area to volume ratio and resultant heat loss, would require greater food allocation for body temperature maintenance (Peters 1993). A prolonged existence at a small body size is characteristic during the protracted development of Procellariiformes. This represents a real cost to adults in terms of the proportion of energy delivered to the colony, devoted purely to ameliorate heat loss, which may result in nestling mortality as discussed in Chapter 5.

#### 4.4.3 Input during nestling development

The mean weight of nestlings, mean weight change and food delivered by adults suggest that 2000 was a more favourable year than 2002. In 2000, pairs appeared able to meet the needs of nestlings, whilst in 2001 in a less favourable year food delivery

was erratic and reduced. However, even in 2001, the food consumed over a 10-day period also displayed the variable needs of nestlings throughout ontogeny, albeit these were met at a much lower level than in 2000. This suggests that the erratic nature of food delivery may aim to achieve an overall influx of food, where large meals ameliorate periods of poor provisioning. During times of deviation from the ideal situation, or optimal provisioning schedule, the total food delivered over a limited period may thus determine nestling success. In 2000, the average weight of the cohort of nestlings increased more rapidly peaked earlier and at a higher mass, than in 2002. Furthermore, in 2002, marked flat spots were noted during the characteristic weight gain phase. This suggests that conditions in 2002 were not favourable, with energy flow to the colony reduced, erratic and often interrupted, and as a consequence nestlings suffered throughout development. Potential implications on growth will be examined in Chapter 5.

In both favourable and less favourable years, adults either varied their provisioning rate with the age of the nestling, or nestlings accepted food only in accordance with their needs. The needs of nestlings would be expected to alter with their size, and therefore age, as weight loss was seen to be dependent upon body size. Metabolic needs vary with body size in relation to thermoregulation (Peters 1993) and developmental stage (O'Connor 1984). Meal size also increased with age for other species, such as the Shy Albatross *Thalassarche cauta* in Tasmania, and then dropped before fledging (Hedd et al. 2001). In the northern hemisphere, an increase in maintenance meal size for Little Shearwaters was detected over a very short period, from 14.6 to 19.8 g from 2 April to 9 April (Hamer 1994). Similarly, at the North-West Shelf, the amount of food required by Wedge-tailed Shearwater nestlings to

maintain a steady weight increased throughout development and subsequently decreased towards fledging, with variability noted between years (Nicholson 2002). This suggests that a nestling may be able to set needs in accordance with the food delivery schedule orchestrated by the parents, upon which they are dependent for their survival.

Frequent weighing provides a profile of provisioning at one time during nestling feeding. In this study, Little Shearwater meal sizes were measured at nearly the same time each year, allowing inter-annual comparison. Maintenance meal size and meal sizes were highest in 2000, lowest in 2001 and intermediate in 2002. This matched predictions where, 2000 was the favourable year, 2001 a transition year, and 2002 marked by reduced current flow. The results indicate that Little Shearwater provisioning and food needs were indeed elevated in the most favourable year. Conversely, in 2002, overall food delivery was highly erratic and reduced throughout development, in accord with less favourable environmental conditions.

It is, however, more difficult to understand why both maintenance needs and meals delivered were lowest in 2001. It is possible that a more even aged, possibly younger, group of nestling had inadvertently been chosen, as indicated by the absence of any influence of body index. However, provisioning rates in 2001 were also lower than in the other years, suggesting that another reason may be more plausible. In 2001, a year marked by fluctuations in SOI, intermittent periods of favourable and less favourable conditions probably ensued and the short-term, intensive sampling period may have coincided with less favourable conditions. However, in 2001 the uncorrected amount of food delivered was also highly variable, as indicated by the spread of uncorrected

meal sizes (Figure 4.2). It is therefore more likely that, in the transition year of 2001, characterised by unstable SOI, a larger proportion of the population, presumably of variable quality were able to participate in reproduction than in 2002. Indeed, 2002 was marked by prolonged cold water and lower participation rates in reproduction, suggesting that only high quality pairs had dependent nestlings in that year.

In this study, meal sizes were recorded for Little Shearwater nestlings in late September to early October, with peak hatching occurring in early September. At this time most nestlings were nearly a month old and the 29.2-32.2 g meal sizes were equivalent to 15.8 – 20.8 % of adult mass. This compares with an average meal size of 23.2 g fed to Little Shearwater nestlings in the Atlantic Ocean in the boreal spring, equivalent to 13.6 % of adult body weight (Hamer 1994). The northern hemisphere study was conducted in early April after peak hatching had occurred in late March (Hamer 1994), implying that the nestlings were approximately one month old. Overall, Little Shearwater nestlings of similar age in the Atlantic appeared to be fed smaller meals than Little Shearwaters in the western region of the Indian Ocean.

Different diets at different locations (Chapter 8), and potential shifts of diets within a season (Chapter 6) may prevent direct comparison of mass, as the weight of a meal does not convey information about its energy and nutritional content. For example, species creating stomach oils during long absences would provide meals of higher calorific content, than other species, or even itself, when returning from short absences when only semi-digested food is regurgitated. The Phoenix Petrel *Pterodroma alba* delivered meals of higher energy content and lower water content to nestlings than the Christmas Shearwater (Ricklefs 1984a). Similarly, a species may

shift diets between years in accordance with prey availability, as documented for Australian Gannets *Morus serrator* during a pilchard mortality (Bunce and Norman 2000). The average meal size delivered evidently varies with nestling needs. Therefore, it may be difficult to compare meal sizes within and between species without reference to age, diet, foraging strategy and also to some index of seasonal changes in oceanographic productivity.

In all years, the corrected meal sizes consumed by nestlings suggested that food delivered narrowly exceeded the mass needed by nestlings to maintain a steady body weight over a 24 h period. This may explain why nestling growth is slow and why Little Shearwaters aim to deliver food nearly daily. In the northern hemisphere, Little Shearwaters required, on average, 16 g of food to maintain a constant mass (Hamer 1994). In our study, maintenance meal sizes were higher (24-32 g), but a direct comparison may not be appropriate as nestling maintenance needs may vary with age, environmental conditions and composition of meals.

During frequent weighing, the number of meals delivered in a night was equal in 2000 and 2002, but lower in 2001. Frequent weighing in 2001 and 2002 was conducted over a three-day period, which is easily affected by weather (Schultz and Klomp 2000) or by cyclic patterns of attendance in species with dual foraging strategies (Weimerskirch 1998) and patterns adopted early during incubation (Brooke 2004). The effects of short-term weather patterns during the short sampling interval may have obscured provisioning. During frequent weighing in 2000, the return of Little Shearwater parents appeared to be weather related. Similar results emerged in Chapter 3. This suggests that short-term sampling has the potential to be very biased.

In 2001 and 2002 frequent weighing was timed to include windy periods and thereby maximise the number of meal sizes recorded for effort expended. This is supported by overall high provisioning rates recorded during frequent weighing, although long-term patterns, typified by the percentage of nestlings fed, suggest that the rate of delivery was markedly lower in 2001 and 2002 than in 2000. Furthermore, the total overnight food consumed and the average real time weights of nestlings suggest that in 2000 the overall amount of food delivered was greater than in 2002.

It seems that Little Shearwaters on Beacon Island attempt, whenever possible, to deliver on average one meal each night to the nestling. In all years, the Little Shearwater nestlings were fed more regularly than many other species of shearwater, such as the Short-tailed Shearwater (Saffer et al. 2000). Similar and even greater visitation rates have been recorded for the species in other studies at different locations: on the eastern coast of Australia *P. a. assimilis* 94 % (Priddel et al. 2003), in the Northern Atlantic *P. a. baroli* 95 % (Hamer 1994) and in northern New Zealand *P. a. haurakeinsis* 90 % (Booth et al. 2000b). However, nestlings in the present study were fed more regularly than members of the same subspecies breeding at a different location. On Eclipse Island off the southern coast of Western Australia, nestlings were fed on average every second night (Glauert 1946). This rate is much lower than that recorded at the Houtman Abrolhos Islands, despite the latter being located at the northern edge of the Little Shearwater's breeding distribution.

The total overnight food accepted by nestlings does not provide any insight into how the system was controlled. It is not known, for instance, if adults only carried smaller meals when the nestling was young, or if the nestling only accepted a small meal.

From a payload perspective, it would be advantageous for adults to return with meals tailored to the needs and capacity of the nestling, as food delivery from distant foraging sites is presumably associated with substantial costs. The notion of parental control is supported by the erratic nature of food delivery observed in 2002, when the nestlings ate what was provided. Such alternations of small and large meals (variable payloads) may indeed be an inefficient system of food delivery, where high payloads are energy expensive and small payloads barely warrant energy expenditure by the adult in terms of gain for the nestling. In favourable years shearwaters may be able to operate an optimal provisioning schedule.

Little Shearwater nestlings were not deserted completely prior to fledging, but did experience decreased provisioning, both in the meal size and its frequency of delivery. Nestlings not fed for several nights before fledging may have had inexperienced parents, been too high in weight or been awaiting weather conditions favourable for their first flight and departure from the island. The data set included one good year and two less favourable years, but did not allow discrimination of several possible scenarios. Firstly, in a good year, more nestlings may be deserted prior to fledging, since even inexperienced and low quality birds managed to participate in reproduction in such years. Secondly, in the least favourable years, more nestlings may be deserted when conditions became marginal and adults opt to conserve their own body condition, despite their large investment. Thirdly, the peak weights reached before fledging may dictate if adults can “desert” their nestling completely. Nestlings that peak at a higher weight may be left unfed earlier by parents, allowing adults more time to recover and prepare for future reproduction. From an investment perspective, it seems unlikely that nestlings are deserted and that post fledgling aid is not granted.



The state of obesity attained may thus serve to gain a direct advantage for the parents, as well as indirect advantages in the form of nestling survival, and will be discussed throughout the thesis.

#### 4.4.4 Flexibility of provisioning during nestling feeding

Provisioning varies with the age of nestling, between years at a breeding location and also between different breeding sites. Once nestlings have surpassed a critical post hatching weight (Chapter 3), provisioning of a nestling can be quite flexible, since it can withstand periods of reduced provisioning. Thereafter, parents do the best they can with the resources available in a given year within an accessible foraging distance. Thus, pairs maintain provisioning at a level that suits environmental conditions, rather than at a flat rate characteristic for their species. This is in keeping with results obtained for Wedge-tailed Shearwaters on the east coast of Australia, where provisioning was reduced during years of elevated SSTs (Smithers et al. 2003). An optimal provisioning schedule may be realised by a species in a favourable year. Deviations occur when conditions are not optimal, in accord with the adults' ability to maintain a threshold weight, and costs are passed on to the offspring.

#### 4.4.5 Potential regulatory mechanism of food delivery

In Little Shearwaters, parents appear to alternate between long absences and periods when one parent returns almost nightly. In 2000, periods when one parent attended to a nestling daily lasted, on average,  $5.9 \pm 1.1$  days (Table 4.5) and prolonged absences lasted on average  $5.2 \pm 1.3$  days. The distribution of absences was indicative of a

dual bimodal foraging strategy (Figure 4.9). Such a foraging strategy was also noted during the retrieval of MDGs in 2002 (Chapter 8, Figure 8.4), when seven long trips lasted, on average,  $8.6 \pm 1.4$  days (range: 6-11). For comparison, the duration of incubation shifts was  $7.7 \pm 1.5$  days in 2002, during which an adult was replenishing body condition lost during incubation shifts when fasting occurs.

The weight loss experienced by individuals engaged in daily provisioning and heavier weights of birds returning from long absences suggest that the long absences serve to replenish adult body condition. This is consistent with findings that the long trips in a dual foraging strategy serve to maintain adult body condition in the Blue Petrel (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 2003), Wandering Albatross (Weimerskirch 1995), Sooty Shearwater (Weimerskirch et al. 1994, Weimerskirch and Cherel 1998), Cory's shearwater (Granadeiro et al. 1998) and Short-tailed Shearwater (Klomp 2000). In the Little Shearwater, adults engaged in periods of daily provisioning regularly visit the nestling and have frequent visual feedback about the condition and needs of the nestling. However, this regular almost nightly, food delivery to the nestling is costly for the adult.

It has been suggested for larger shearwaters that, during short foraging trips, the nutrition of the parent is negligible (Weimerskirch et al. 2003). This may account for the gradual drop in post-feeding adult weights recorded during daily attendance. However, energy demands associated with food delivery may be elevated through daily travel between breeding sites and potentially mobile and ephemeral foraging sites. Therefore, the adult may be working extremely hard, and losing condition, despite metabolising food to sustain the activities. Little Shearwaters, being smaller

than most conspecifics, have a lower safety margin in terms of weight loss before a threshold is reached. It is possible that parents withhold some food from the nestling and that they use the prolonged period on the island at night to digest this, since digestion is often hampered during flight (Peters 1997 cited in Ropert-Coudert, 2004). This may explain why Little Shearwater adults are present for most of the night, even during less favourable years, unlike other shearwaters, which depart soon after feeding the nestling. Alternatively, there are no incentives to depart at night, for example their prey may not be accessible at night.

In a favourable year, 75 % of Little Shearwater nestlings were fed within the first third of the night although parents remained on Beacon Island until dawn. However, during the less favourable years, more adults arrived later at night, possibly because it took longer to obtain food and return to the colony. A shift in foraging locations that directly affected breeding success has been recorded in other studies (Inchausti et al. 2003). There were some indications that the duration of long absences during nestling feeding in 2000 were shorter than those recorded in 2002. This is consistent with 2000 being a more favourable year and may explain why parental provisioning suffered in adverse years and should be examined further. In Audubon's Shearwaters, the duration of incubation shifts was longer in years of lower food availability than during favourable years (Harris 1969a). During incubation, adults also use absences from the colony to replenish reserves lost during provisioning. Foraging strategies therefore appear to be malleable in terms of the time needed to replenish body reserves, and strongly affected by environmental conditions, a topic that requires further investigation.

Further research should focus on the duration of long absences used to replenish body condition. Automated means to record the attendance of individual birds may be more suitable to record changes in the duration of absences during favourable and less favourable years. Automated means can monitor a larger number of pairs over a longer period of time with minimal impact (Granadeiro et al. 1998). Similarly, in a given year, some adults took longer than others to replenish body condition and therefore not all pairs were able to co-ordinate a near daily feeding regime suggesting variations in quality exist between individuals and pairs. The resultant variability in input between different pairs may result in nestlings of variable quality and chance of post-fledging survival (Chapter 5).

Foraging strategies do not appear to be fixed within a species operating at different locations, but rather provide testimony to the prevailing oceanographic conditions and the need to maintain parental care to achieve genetic persistence, whilst primarily protecting the body condition of the adult, and possibly the pair. The Wedge-tailed Shearwater at Hawaii adopted a unimodal foraging strategy (Baduini 2000).

However, the same species at the Great Barrier Reef adopted a dual foraging strategy to compensate for poor local food availability by targeting distant resources (Congdon 2003). In both situations, nestlings were fed regularly, although the foraging strategy differed.

At Beacon Island, Little Shearwaters provide a nearly nightly delivery of food using a dual bimodal foraging strategy. Longer absences at sea would allow individuals to target distant resources, beyond the foraging range achievable during the 12-20 h period at sea available during periods of daily provisioning (Chapter 8). This would

reduce competition between adults for food and possibly enable access to areas of high productivity. However, this does not imply that Little Shearwaters breeding at the south-western coast of Western Australia necessarily use the same foraging strategy.

In 2000, the change-overs between adult Little Shearwaters engaged in long absences and periods of daily provisioning were highly co-ordinated and nestlings were rarely left unfed. In New Zealand, Little Shearwaters *P. a. haurakeinsis* also used a co-ordinated dual foraging strategy (Booth et al. 2000b). The co-ordination of parental efforts is most likely to be foremost state-dependent, whilst the cues for change-overs may be weather related as this allows energy conservation. Decision making in Antarctic Petrels may take into consideration the state of the nestling, the adults body condition and that of its partner. Here, parents with higher body mass were better able to co-ordinate guard behaviour than lighter pairs (Varpe et al. 2004).

During a period of daily provisioning, the attending parent may have failed to return for a night, suggesting that proximal conditions were not suitable or that its body condition was being protected. The latter appears less likely as the phenomenon occurred at different weights, at times within a period when adults would expect to lose weight, and no distinct rise in post-feeding adult weights was detected indicative of direct adult gain after a missed night. No significant relationship was detected between weather and the number of nestlings left unfed, which suggests that the temporary disruption in food transfer was unlikely to stem from the lack of energy-efficient, weather-assisted transport. Rather, absences of one night during the period of daily provisioning probably result from insufficient food available at a comfortable

daily flight distance. On the east coast of Australia, food resources were observed to fluctuate with small-scale variations in SSTs. As a result fine-scale changes in SSTs may influence reproductive success in Wedge-tailed Shearwaters, as well as long-term, large-scale climatic El Niño conditions which are associated with stable and prolonged changes in SSTs (Peck and Congdon 2003).

In this study, the nightly weight differences recorded for nestlings at the start of a period of daily attendance appeared to be similar throughout the whole period of attendance by that adult. Distinct increases in food delivered to the nestling were only observed when both adults were encountered at the nest. This should be investigated in more detail. For example, it is not known if Little Shearwaters deliver energy-rich, light-weight stomach oil after a long absence, which would alter the energetic content per unit of food and confound direct comparison by mass alone. Stomach oil represents an energy-rich, but nutrient-poor meal, whereas after daily absences, the fresh food delivered contains all nutrition essential for growth (Weimerskirch et al. 1994).

During change-overs when both parents visited in a night, nestlings often received large meals, that were thought to represent two meals, one from each of the parents. However, often the amount of weight lost by the adult arriving after a longer absence was less than its partner at the end of a period of daily provisioning. It is possible that adults returning from long absences arrived later in the night than those provisioning daily, by which time the needs of the nestling had already been met. Four hour sampling intervals may have been too large to determine this. Alternatively, the lower feeding rate helped to conserve the body condition of the parent, that would

have to provide for the nestling daily for a lengthy period of time. Overlap between the adults also signalled that the individual attending daily relieved its partner before reaching a minimal threshold body condition. The departing adult would derive little benefit in carrying extra weight out to the foraging grounds and, by feeding its nestling, would offload any remaining food, to allow energy efficient travel to a distant foraging site.

Since most adults were relieved by their partner, the weights of adults departing for long absences do not necessarily represent threshold weights. Evidently, some individuals continued daily provisioning before departing, and both adults then attended to the nestling for a couple of nights. Other change-overs occurred without overlap. In these, the adults fed nestlings daily until their body weight had dropped to a critical level or a favourable section of a weather system appeared. Whereupon they decided not to return to feed their nestling and the partner resumed daily feeding the next night, seemingly without communication. It was observed that during the passage of a front change-overs between partners were more likely to occur (Figure 4.7). Thus, the return of adults after long absences, and the departure of the adult previously attending the nestling, may be linked to weather conditions created by the near cyclic conditions created by the weather patterns experienced on this coast. This suggests that the provisioning system may be entrained by some recognisable, but remote mechanism, such as weather, that minimises adult energy expenditure.

In winter a succession of cold fronts pass over the area at a near regular basis, occasionally punctuated by a large high pressure cell. On average at least one front is

expected each week in spring, although not all influence the lower latitudes. The predictable winds generated by the weather systems may create conditions that allow birds to minimise energy expenditure during travel. However, only birds whose ability to replenish energy demands within the temporal pattern set by the spacing of weather systems, will be able to benefit. Others, possibly less experienced birds, which at some point failed to reach a comfortable weight, lose synchrony with the weather patterns. This may result in two scenarios: return during less favourable weather conditions to tend to the nestling, whereby adult energy loss occurs.

Secondly, the bird can continue to stay away from the colony until favourable conditions arrive, at this time the adult engaged in near daily provisioning would have departed to protect its body condition. Weather assisted travel has been documented in Short-tailed Shearwaters (Klomp 2000) and may be a feature of distant foraging, whilst birds or species foraging locally can return anytime with minimal penalties on energy expenditure.

Individual weather variables are difficult to measure at an island, as these may be limited in their ability to define the cue of importance to the birds and are difficult to relate to the unknown foraging location. At the West Australian coast weather systems arrive from the west and the birds may have experienced a trigger at a distant location well before the system arrives at the island. Satellite tracking and monitoring of broad weather systems has shown how the distribution of non-breeding Wandering Albatross is influenced by weather systems (Nicholls et al. 1997) and that Short-tailed Shearwaters hitch rides on winds associated with weather systems (Klomp 2000). Unfortunately, the cost and weight of tracking devices were beyond the scope of a study of Little Shearwaters.



The return of birds from sea was assisted by favourable weather systems during incubation and the transition to nestling feeding (Chapter 3), as well as during frequent weighting. It would be interesting to ascertain if individuals returned at similar maximal weights from successive long absences, which would have implications for the period over which they are able to feed their nestling nightly. It also introduces the potential need for departing individuals to take into account not only their own body condition, but also that of their partner and thereby safeguard future reproductive potential in a system marked by prolonged, biparental care (Brooke 2004).

The weight loss experienced by adults while provisioning their nestling daily varied between individuals. In this study, the provisioning patterns of males and females were not compared, owing to an inability to reliably differentiate the sexes. Sexual dimorphism in Little Shearwaters is often small and overlap common. For 12 of 21 pairs studied intensively in 2000, the morphometric measurements were too close to determine the sex reliably, using the assumption that females chose larger males. Here, measurement errors alone could have reversed the sex of partners within pairs. DNA samples have been collected and await the resources needed for analysis. In Manx Shearwaters, sex-specific provisioning has been detected, with males delivering more food to the nestlings and absent from the colony for shorter durations than females (Gray and Hamer 2001). Similarly, difference in provisioning between male and females was detected in Wandering Albatrosses (Berrow and Croxall 2001). Also, female Wedge-tailed Shearwaters terminated provisioning earlier than males

during the pre-fledging period (Baduini 2002). Sex- specific differences in provisioning might be a fruitful area for further research.

#### 4.4.6 State-dependent co-ordination of parental care

In the Little Shearwater, it appears as if the pair aims to feed the nestling daily. Any deviation from this optimal provisioning pattern indicates a pairs' inability to operate above a threshold adult body condition with prevailing environmental conditions. As conditions deteriorate, a smaller proportion of pairs are able to maintain a uniform, co-ordinated system of food delivery and the nestling is fed less than optimally.

In most phases of provisioning, adults are expected to absorb declines in adult body weight associated with reproduction, down to some threshold weight. In a favourable year, adult body condition can easily be replenished to cover repeated drains by elevated demands. Therefore, adults have the capacity to meet nestling needs closely, as evident in 2000, when food delivery consumption by nestlings mirrored their pattern of weight gain. The ability to adjust provisioning in accordance with nestling needs has been observed in many other studies (Bolton 1995, 1995b, Hamer and Thompson 1997, Bradley et al. 2000). During such years birds may also be able to react to increased demands at the nest.

During a less favourable year, adults may struggle to gather sufficient energy to cover the elevated needs and maintain adult weights above a threshold weight. As a result, Little Shearwater adults appeared unable to meet the needs of the nestling in a less favourable year. This suggests that adults will shunt costs to the offspring (Muck and Grubb 1995) whenever conditions make it difficult to meet their own needs. Overall,

adults are able to respond to nestling needs, providing their body condition allows (Tveraa et al. 1998). Such state-dependency has also emerged in studies focusing on the adult's ability to co-ordinate guarding of hatchlings (Varpe et al. 2004).

At the Houtman Abrolhos Islands, food delivery was adjusted to suit nestling needs in good years and adults appeared to co-ordinate provisioning, albeit within the limitations needed to maintain adult body condition. An underlying threshold adult body condition has been proposed in many studies (Tveraa, 1998; Granadeiro, 1998). In contrast, in the northern hemisphere, Little Shearwater meal size and feeding frequency appeared not to be adjusted to the nutritional status of the nestling. Rather, provisioning patterns, determined over a relatively short period of time, suggested that adults acted in accordance with intrinsic rhythms, independent of the nestling (Hamer 1994). This is in keeping with several manipulative studies, in which increased demand at the nest was not met (Ricklefs 1987, 1992, Hamer and Hill 1993). Unfortunately, most studies of Procellariiform provisioning have not been anchored to an index of oceanographic productivity. The often conflicting and contradictory outcomes noted might have arisen through interpretation of results in the absence of environmental conditions, which may have prohibited a reaction to increased demands at the nest in one year, but not in the next year. Seabirds operating a state-dependent system of provisioning will react in accord with the limitations imposed by the environment.

Provisioning appears to be a flexible behaviour, which allows long-lived, iteroparous species to react to proximal conditions, and ultimately, to breed in both stable and also less stable environments. Foremost provisioning is state-dependant and movements

when possible, may be assisted by favourable weather systems, when travelling to and from distant foraging locations. The Western Australian coast can be viewed as a highly unpredictable oceanographic region, where state-dependent reactions are more likely to surface. The deviation from an optimal provisioning schedule may influence nestling growth this is examined in Chapter 5.

## **5 Chapter 5: Nestling growth in Little Shearwaters**

### **5.1 Introduction**

The growth of the dependent nestling is influenced by the quality and quantity of food and the rate at which it is delivered by the parents. In this study, food delivery was adjusted to meet the changing needs of nestlings with age. Furthermore, inter-annual differences in provisioning were detected, where adults adjusted the amount of food delivered and the regularity of delivery in different years (Chapter 4). This chapter focuses on the implications of this disruption to the input system in adverse years, or a potential deviation from an optimal provisioning schedule based on co-ordinated parental care.

Growth parameters, other than weight, are thought to be heritable (Ricklefs 1968, 1973, 1979), but are also affected by the parents' ability to cope with proximate factors, such as environmental conditions. The growth of nestlings was monitored at regular intervals, allowing the weight patterns of known-age nestlings to be presented and used to comment upon obesity. Little Shearwaters feed their nestlings more regularly (Hamer 1994, Booth et al. 2000) than some other shearwaters, so that large lipid or other accumulations of food reserves should not be required as a buffer against periods of lack of food delivery. However, the susceptibility of the Western Australian coast to variations in SOI and resultant resource unpredictability (Chapter 1) suggests that adults should feed nestlings while they can. Global growth

curves were therefore produced for the skeletal and plumage growth of known-age nestlings in each of the three years and compared to determine inter-annual variation.

## **5.2 Methods**

### **5.2.1 Linear measurements**

Nestlings were weighed twice daily and measured when possible. In 2000 and 2001, measurements were taken once a week, whereas in 2002, measurements were obtained at intervals of 3 to 7 days to ameliorate a small sample size. No control groups were used, since repeated human handling and other disturbances have been shown not to alter growth patterns in Short-tailed Shearwaters (Saffer et al. 2000).

Skeletal measurements were taken using vernier callipers, including the head and beak length, culmen length, tarsus length and the bony part of the wing (starting at the region where the ulna meets the carpometacarpus to the end of the phalanx II of the second digit). As in most studies, wing length was measured, which included the length of the bony part of the wing and the growing plumage. To supplement this, the bony part of the wing was also measured (wing bone), and the 5<sup>th</sup> covert. In one year, the eruption of scapular feathers on the back of the nestling, between the shoulder blades, was measured and its transition from egg down (or protoptile) to thick down (or mesoptile), and then to contour feather was monitored. Some plumage measurements were time consuming, especially for mesoptile under windy conditions, and were abandoned in subsequent years. Before fledging, the loss of mesoptile was also documented by estimating the percentage remaining. This loss occurred very suddenly and, in retrospect, should have been monitored at more regular intervals.

### 5.2.2 Logistic growth curves: individual and global

Global growth curves were created for each year based upon values for all nestlings of known-age, which were measured within each year at regular intervals from hatching to fledging. Repeat measures taken of individual nestlings have been used to create growth curves for other procellariids (Ricklefs 1968, 1973, Weidinger 1997, Saffer et al. 2000). The growth patterns can be described by different models within a family of sigmoidal growth curves, such as the logistic, Gompertz and von Bertalanffy growth curves. The logistical growth curve suits symmetrical patterns and assumes a point of inflection at 50 % of the final value reached by the parameter measured. The other two growth curves are asymmetrical and suited to variables with rapid growth early in development. All three models have been applied to procellariid growth, with the logistic curve found to be most appropriate for standard measurements such as head length, beak length, tarsus length and wing length (Weidinger 1997, Saffer et al. 2000). Consequently, the logistic growth curve was used in this study. Initial phases of growth cannot be measured as they occur within the egg. A logistic growth curve was fitted to the data using the non-linear regression featured in SPSS Advanced Statistical Package for Windows:

$$\text{Size} = A / [ 1 - \exp ( - K T ) ]$$

Where:

A is the asymptotic size of the measured parameter (g or mm)

K is the instantaneous rate of growth of the parameter (mm per day<sup>-1</sup>)

T is the point of inflection at 50 % (days from hatching)

The non-linear regression generates a least squares fit to the data using an iterative algorithm. The latter is then assessed for fit, firstly by the magnitude of the residuals,

then by convergence and visual appraisal. This method has been used for Little Penguins *Eudyptula minor* (Weidinger 1997), Short-tailed Shearwaters (Saffer et al. 2000), Flesh-footed Shearwaters (Powell 2000, 2004) and Wedge-tailed Shearwaters (Nicholson 2002).

Logistic growth curves were fitted to individual data sets of known-age nestlings for different linear measurements, provided that more than four data points were available. Also global growth curves for these linear measurements were produced for the combined data from all known-age nestlings in each year. The global curves ameliorated the bias associated with repeat measures of the same individual and with differences in individual growth. The global curves will later be used to depict growth patterns of Little Shearwater (Chapter 5) and Wedge-tailed Shearwater (Chapter 7) nestlings.

### 5.2.3 Comparison between years

When sufficient data were available for 2000, 2001 and 2002, the differences in growth parameters of known-age Little Shearwater nestlings were compared between the three years using the residual sum of squares. As an alternative the more powerful Akaike's Information Criterion (AIC) could have been used. The AIC has been strongly advocated and should be the sole tool for selection of the most appropriate model, when testing a nested series of models (Burnham and Anderson 2002).

However, the purpose of this analysis was simply to test the presence of significant year effects in the parameters of the model, rather than to select the most ideal model. Consequently, the analysis restricted itself to significance tests and did not make use of the AIC.



## 5.3 Results

### 5.3.1 Weight gain

The average weight of known-age nestlings followed a pattern typical for procellariids. A stage of obesity was reached after approximately 70 % of the nestling period (Figure 5.1). Thereafter, weight was lost. A state of obesity was reached in all years. Weights peaked in some nestlings as early as 28 October, while most nestlings reached maximal weights between 02 and 10 November. Maximal morning weights of 289 g, 281 g and 281 g were recorded in 2001, during visits on 03 and 13 November. Since sampling was intermittent, higher morning weights could have been reached at other times.

In 2001, the average maximal weight of eight nestlings was  $269.5 \pm 14$  g (range 252-289 g). In 2002, some nestlings never achieved a maximum weight above 200 g. Considering only those exceeding 200 g, an average maximum weight of  $250.75 \pm 17.2$  g ( $n = 12$ , range: 213 - 275 g) was attained. Thus, although 2002, was a less favourable year for Little Shearwater reproduction, some nestlings still reached a state of obesity.

Global growth curves were created for 2000 and 2002, the years with more complete data sets available for nestling weights (Figure 5.2). Comparison of these growth curves suggested that, in 2000, nestlings gained weight more rapidly than in 2002. In 2002, peak mass was lower and nestlings fledged after a longer period at lower weights than in 2000 (Figure 5.1). Clearly 2002 was a less favourable year than 2000 for nestling growth in terms of weight gain. The global growth curves also display this (Figure 5.2). The associated parameters show that, in 2000, the rate of weight

**Figure 5.1** Regular, daily fluctuations in average weights were recorded for known-age nestlings on Beacon Island in 2000 and 2002.

**Figure 5.2** The global logistic growth curves fitted for the weights recorded for 26 known age Little Shearwater nestlings in 2000 and 23 known age nestlings in 2002.

gain was greater and time taken to reach a point of inflection was shorter than in 2002. However, the asymptote reached in 2002 was greater than in 2000 and the suitability of the logistic growth curve for dealing with pre-fledging weight regression will be discussed later.

### 5.3.2 Fledging weights and period

In 2000, an average fledging weight of  $180.5 \pm 17.7$  g was recorded for 17 nestlings (range: 152-218 g), while in 2002 an average fledging weight of  $177.6 \pm 28.2$  g was recorded for seven nestlings (range: 156-233 g). Nestlings were measured at 17:30 h before their nocturnal departure from Beacon Island. Fledglings appeared to depart before midnight, since many Little Shearwater fledglings were encountered on a charter vessel at night.

On 23 November 2000, fledglings were encountered near Leo Island, which has one of the largest Little Shearwater rookeries in the Houtman Abrolhos Islands. The nestlings were disorientated by the bright mercury-vapour lights of a vessel and crashed onto the deck between 21:00 h and midnight. The birds, presumed to be recent fledglings, still carried traces of down. The average weight of these nine juveniles was  $179.6 \pm 11.1$  g (range: 163-197 g), very similar to the weights of nestlings on their last night down a burrow. In 2000, an average fledging period of 72 days (range: 68-74 days) was documented for 17 nestlings, marginally shorter than the average fledging period in 2002 of 74 days for 7 nestlings (range: 70 - 78 days).

### 5.3.3 Skeletal and feather growth

Global logistic growth curves for head and beak, tarsus, culmen and total wing length displayed a pattern typical of other procellariids (Figure 5.3). The tarsus matured earliest, culmen and head-beak length matured later, with the wing reaching maturity most slowly. Interestingly, the wing bones matured well before the wing, which included plumage growth and inter-annual differences were apparent for most measurements.

Different values of A, K and T for global logistic growth curves for each parameter best described the data set collected over the three years (Table 5.1). Generally, growth rates were greatest in 2000 and lowest in 2001, but asymptotes reached in 2000 were often smaller than those reached in 2002. Significant differences were detected when attempting to define the data from the three years using common values for A, K and T (Table 5.2).

Interestingly, only tarsus length varied little between years. Tarsus length can be defined by a common asymptote and growth rate however, if both were fixed, significant differences from the global model were detected (Table 5.2). For wing bone, a common asymptote was not reached in the three years, despite growth rates being similar. The rate of wing growth was significantly different between years, but reached a similar asymptote. However, the asymptote calculated using the logistic growth equation greatly exceeded adult wing length, and was therefore unrealistic, owing to the lack of repeat measurements obtained near the end of the fledging period, near the asymptote.

**Table 5.1** The logistic growth curves descriptors determined for Little Shearwater nestlings in 2000, 2001 and 2002

**Figure 5.3** The logistic growth curves of different body components fitted for known age Little Shearwater nestlings measured in 2000, 2001 and 2002.

**Table 5.2** A goodness of fit for growth data obtained for Little Shearwaters in 2000, 2001 and 2002 where values for each of A and K were allowed to vary for each year relative to a global logistic growth curve when a common rate of growth (K) and asymptote (A) was used for the three years.

Measurement	Common factor(s) across years	F-value	Degrees of Freedom	P-value	Different from global model
Head bill	K	5.93	2	0.0028	**
	A	7.95	2	0.0004	***
	K and A	7.51	2	0.0000	***
Culmen	K	3.69	2	0.0255	*
	A	4.67	2	0.0096	**
	K and A	3.54	2	0.0072	**
Tarsus	K	1.90	2	0.150	n.s.
	A	0.588	2	0.556	n.s.
	K and A	3.374	2	0.0095	**
Wing bone	K	0.127	2	0.881	n.s.
	A	3.428	2	0.033	*
	K and A	4.467	2	0.0014	**
Wing	K	3.269	2	0.0386	*
	A	1.206	2	0.3002	n.s.
	K and A	3.266	2	0.0114	*

The logistic growth curves fitted for head-beak length and beak length indicated inter-annual differences in growth rates and asymptotes reached (Figure 5.3). For both variables growth rate was greatest in 2002, less in 2001 and lowest in 2000. For head-beak the greatest asymptote was reached in 2002, followed by 2000 and smallest in 2001. For beak length the greatest asymptote was reached in 2002, followed by 2001 and smallest in 2000 (Table 5.2). This suggests that the data gathered in the three different years deviated significantly from models with common K and A.

During skeletal growth, the egg down (protopile) with which the nestling hatches was supplemented by a thick secondary down (mesoptile), that was slate grey all over, and



later by contour feathers. Feathers grew out, in a continuous nature, from the same follicle that gave rise to the original egg down (Figure 5.4).

Feather growth occurred continuously throughout ontogeny. Scapular feather growth (Figure 5.5) illustrates how mesoptile grows first, followed by the contour feather.

Wing growth is traditionally measured as the elongation of the whole wing (Figure 5.3). However, the growth of both the bone and flight feathers (initially the primary coverts and later the primaries) were measured separately (Figure 5.6). The growth of the wing bone ceased by approximately 40 days of age (56 % of the nestling period). Thereafter, growth of the flight feathers, such as coverts, primaries and secondaries occurred. The secondaries were not measured. The primary covert reached its asymptote early, at 60 % of the nestling period. Thereafter, the elongation of the whole wing could be accounted for solely by the growth of the primaries (Figure 5.6).

Similar patterns of plumage growth were followed in each of the three years (Figure 5.6). However, in 2002, the onset of feather growth in the wing appeared delayed compared to 2000 and 2001; this will be discussed in the synopsis. The tail contour feathers also grew only during the second half of the nestling period (Figure 5.7), starting around 40 days old (56 % of the total fledging period) and continuing until fledging. During life in the burrow, the thin egg down is worn off and prior to fledging the secondary down is shed, with maximal loss occurring after 60 days old (83 % of the nestling period) (Figure 5.8). In some nestlings, contour feathers grew with fret-marks, or stress lines of inferior structural integrity, which often extended across the barbules and barbs; and in severe cases, the rachis was also affected.

**Figure 5.4** Feathers grown by Little Shearwater nestlings, composed of the protoptile, mesoptile and contour feather.

**Figure 5.5** The growth of mesoptile and contour feathers from dorsal scapular feather tracts in 22 Little Shearwaters in 2000.

**Figure 5.6** The wing growth pattern of known-age Little Shearwaters, showing separately the growth of the total wing and the wing bone.

**Figure 5.7** The tail feather growth in known-age Little Shearwater nestlings on Beacon Island in 2000, 2001 and 2002.

**Figure 5.8** The shedding of mesoptile (down) in known-age Little Shearwater nestlings before fledging

## 5.4 Discussion

Differences in growth rates and asymptotes were detected between the years for most measurement, except tarsus length. Weight gain is very labile, and more likely to be influenced by food availability, unlike other parameters, which are potentially genetically determined (Ricklefs 1968, 1973). However, deviations from potential growth rates were evident. Development of nestlings can be determined by the input system operational during the parental provisioning, however different levels of provisioning may already arise before the nestling has hatched. Differences in breeding participation were registered between the years, being highest in 2000 and lowest in 2002. It is therefore possible, that in 2000 resource levels were elevated and eggs laid were larger and of higher quality. Larger eggs hatch larger nestlings and generally grow to greater weights (Weidinger 1997) and are more likely to survive (Amundsen et al. 1996, Weidinger 1997). Possibly, adults invest less, and produce a smaller fledgling, in years of less favourable conditions.

The pattern of weight gain by known-age nestlings suggests that 2000 was a more favourable year than 2002, during which weight gain was slower, peak weight was lower, fledging weights also potentially lower, and the nestling period was slightly prolonged. These are indications that, in 2002, adults did not deliver as much food to the nestling to facilitate smooth and rapid growth as documented in 2000. Similar results could be gleaned from the global growth curves of nestling weights in 2000 and 2002, which were La Niña and El Niño years respectively.

Two methods, the average weights and logistic growth curve, were used to display weight gain and were inherently different. The logistic growth curves suffered from an inability to accommodate the peak mass and its subsequent regression before fledging (Huin and Prince 2000). According to the global logistic growth curves, weight gain varied between years, but young fledged at a similar weight, as indicated by the same asymptote. This is in keeping with the idea that there is an optimal flying weight for birds. However, despite their differences, both methods suggested that the growth rates of Little Shearwater nestlings suffered in less favourable years, and adults presumably passed on any costs experienced during the year to the nestling.

Despite being fed regularly, nestlings still reached a state of obesity. The maximum weight of 289 g or 169 % of adult weight was reached in 2001. It is possible that similar weights were reached in 2000 and 2002, when sampling was intermittent. Nonetheless, in both 2000 and 2002 nestlings reached weights well in excess of fledging weights (Figure 5.1), even though 2002 was a less favourable year. In both years, the time elapsed between peak weights and fledging appeared similar, as did the margin of weight loss in this period. It is possible that nestlings engage in an activity of fixed duration after peak mass has been reached, that is accompanied by a standard loss in weight. Other studies suggest, that it is a loss of water, rather than a reduction in dry mass or lipid, that accounts for the weight recession prior to fledging (Phillips and Hamer 1999, Reid et al. 2000, Powell 2004). Thus, nestlings would fledge with a lipid reserve that might increase their survival chances (Powell 2004).

Little Shearwater nestlings peaked at weights above adult weight in parallel studies (Booth et al. 2000, Priddel et al. 2003). *P. a. assimilis* on Lord Howe Island peaked at



272 g after 48 days, before fledging at 158 g (Priddel et al. 2003). Since Little Shearwaters regularly fed their nestlings. Booth *et al.* 2000 considered unlikely it that obesity serves to offset irregular provisioning, as a result of meagre, distant, fluctuating ocean resources (Lack 1968, Ashmole 1971). Chapter 4 demonstrated that adults attempt to maintain a regular system of food delivery, but deviations can occur during adverse conditions. The Western Australian coast is characterised by instability in oceanographic conditions that can arise within a given breeding season, linked to global climate. Mass mortality of Wedge-tailed Shearwater nestlings was recorded at the North-West Shelf when conditions deteriorated during one breeding season (Integrated Shearwater Monitoring Program 2006).

Before fledging, a nestling needs to lose weight in order to fly, and generally fledges at an average of 107 % adult weight. Similarly, the weights of recently fledged, free-flying young were very similar to adult weights. The mass recession was accompanied by a reduction in provisioning frequency, but a period of complete desertion was not recorded (Chapter 4). Just 12 days before fledging, 80 % of nestlings were still being fed, a frequency that decreased to below 50 % only two nights before fledging.

Both the weight gain and linear growth of Little Shearwater nestlings were similar to other Procellariiform nestlings (Warham 1990, Saffer et al. 2000b), as was the growth of Wedge-tailed Shearwaters at Lancelin Island in 2001 (Chapter 7). The insulation of the burrow and the thick, secondary down may ameliorate temperature loss and effectively reduce the energy required from adults for nestling thermoregulation.

Since it is otherwise energetically expensive to be of a small body size, in terms of heat loss (Peters 1993), both factors may support the slow development of nestlings.

Interestingly, tarsus growth rate and asymptotes did not differ significantly between years. As expected during shearwater growth, tarsi matured early. This suggests that the tarsus helps perform a vital function and is worth a fixed investment. In the burrow, the rapid development of the tarsus possibly aids in thermoregulation by enabling nestlings to move around in the burrow, as well as to allow the nestling to escape from collapsed burrows (Saffer et al. 2000). However, during dry years on the Western Australian coast, colony stability was low and burrow collapse was frequent. No Little Shearwater or Wedge-tailed Shearwater nestlings were observed to dig themselves out. One Little Shearwater was entombed and subsequently lost so much weight that it became unviable. Similarly, one Wedge-tailed Shearwater nestling remained buried to its head, awaiting rescue. Developed legs may also allow nestlings to move around and to defecate away from the core nest site. This would increase hygiene, decrease parasite loads and decrease the likelihood of soiling the growing feathers.

One cannot suggest that there is a skeletal growth phase and a plumage growth phase, although feathers essential for flight (primaries, secondaries and tail) grow only in the second half of development and may be resource expensive to form, both in terms of essential amino acids for structural integrity and heat loss during formation. Different parts of the body grew different types of feathers and overall feather growth never ceased. Wing coverts erupted, grew and matured before primaries.

The asymptote reached by wings during growth is difficult to define using a logistic equation, since birds often fledge before an asymptote is repeatedly measured.

Hence, unrealistically large asymptotes were calculated for both Little Shearwaters and Wedge-tailed Shearwaters (Chapter 7). However the wings grew significantly slower in 2002 compared to 2000. Since the growth rate of the wing bone could be defined by a common  $K$ , it is possible that the difference in wing growth was produced by slower growing feathers, rather than bone. It is possible that feathers grew slower in the less favourable year, when nestling were fed less.

At the time when feathers essential for flight are formed, nutrient requirements may peak. Furthermore, energy loss may be high, as many feathers are metabolically active and engorged in warm blood. It is possible that obesity is a by-product of nutrient limitations. Indeed, some nestlings had plumage that suffered from structural defects, suggesting that provisioning was inadequate (Bortolotti 2002). Such weak points may result in the need to replace plumage sooner after fledging than would otherwise have been necessary if parents had invested in a higher quality plumage for their offspring. This would place high energy and nutritional demands on a recently fledged bird that is still trying to learn to survive at sea, whilst its flight and hunting performance is compromised. The contour tail feathers grew last; like other flight feathers these are not essential in the burrow and are likely to become soiled and worn by contact with the ground. The major growth of flight feathers occurred after skeletal measurements had reached an asymptote. This delayed growth of feathers essential for flight performance may prevent damage to the feathers on land, as they are essential for survival at sea and difficult to replace, especially for a novice forager.

Little Shearwater nestling weight gain and growth rates differed between years, being lowest in 2002 and highest in 2000, a favourable year. Furthermore, in 2002, the onset of wing feather growth appeared to occur later in the nestling period than in 2000 and 2001. This suggests that adults adjust provisioning annually to suit proximal conditions sufficiently to affect growth of other parameters, not just weight, which was expected to fluctuate. Annual variations in average growth rates have been detected for Wedge-tailed Shearwaters at Hawaii (Pettit et al. 1984) and Little Penguins (Weinecke et al. 2000), whereas Manx Shearwaters in Wales showed little variation (Harris 1966).

Finally, although dimensions and growth rates of nestlings differed between years, the overall patterns of nestling growth in Procellariiformes followed a seemingly predetermined pattern. The differences in growth rates noted between years suggest that adult Little Shearwaters allocated resources differently in favourable and less favourable years. During years of increased SSTs, Wedge-tailed Shearwaters also decreased parental provisioning, resulting in decreased growth rates (Smithers et al. 2003). In other studies too, Procellariiformes consistently regulated provisioning to maintain adult body condition (Lorentsen 1996, Tveraa et al. 1998, Takahashi et al. 1999, Takahashi et al. 1999b), while any costs were shunted to the nestling (Muck and Grubb 1995, Smithers et al. 2003). Although decreased growth rates are associated with decreased provisioning, this did not necessarily translate into smaller birds, however, plumage growth may be adversely affected. It is possible that the ocean exerts a strong selective stabilising force (Bull 2004) that encourages specific adult dimensions, whilst plumage may be exchanged later by the nestling, whilst foraging at sea, to attain adult plumage dimensions.

## **6 Chapter 6: Wedge-tailed Shearwater parental provisioning during nestling feeding**

### **6.1 Introduction**

This chapter investigates selected aspects of parental provisioning in the Wedge-tailed Shearwater for later comparison with the Little Shearwater in Chapter 9. Unlike, the Little Shearwaters, Wedge-tailed Shearwater adults often leave the colony soon after feeding the nestling therefore it was not feasible to study adult patterns of attendance and weight loss. Consequently, patterns of food delivery by Wedge-tailed Shearwaters were monitored only indirectly through the weight increases of the nestlings and viewed in the context of weather systems. Proximal weather conditions have the potential to change energy expenditure associated with foraging (Brooke 2004).

The main study of growth in Wedge-tailed Shearwater nestlings was in 2000/2001, when conditions facilitated Wedge-tailed Shearwater reproduction off the west coast of Western Australia (Chapter 1) (Wooller et al. 1991, Integrated Shearwater Monitoring Program 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, Surman 2002, Integrated Shearwater Monitoring 2006). During this year adults were expected to meet nestling needs. Research results (Table 1.4) and other studies of the Wedge-tailed Shearwaters along the Western Australian coast suggested that 2001/2002 season was less favourable for reproduction than the 2000/2001 season (Integrated Shearwater Monitoring Program 2002, 2003). In 2001/2002 Wedge-tailed Shearwater reproduction nestlings were also monitored

during the pre-fledging weight loss period. During a less favourable year adults were expected to struggle to meet nestling needs and possibly desert their nestling early.

Stable isotope analysis is time-dependent, with feathers used to track the diet, and the foraging location, of individuals during moult (Thompson and Furness 1995, Cherel et al. 2000, Bearhop et al. 2001). In Chapter 8, the egg membrane composition of Wedge-tailed Shearwater eggs is presented and compared to the Little Shearwater. This will give insight into the foraging behaviour of females during egg membrane formation. Here, stable isotope analysis was used to determine the composition of feathers grown at different times of the season to provide insight into the diet of nestlings and indirectly the foraging behaviour of adult Wedge-tailed Shearwaters during nestling feeding. This serves to examine the validity of comparing meal sizes received by nestlings using mass alone, since a shift in diet may result in differences in nutritional and energy returns per unit mass.

In other years, shorter periods were used to explore the relationship between the adult and the nestling, by means of supplementary feeding (Harris 1978, Takahashi et al. 1999, Bunce and Norman 2000, Grieco 2001) and respirometry. Respirometry was used to approximate the resting metabolic rate using the respiratory quotient (Withers and Williams 1990) of nestlings during the pre-fledging period. It was expected that metabolic rate would change with feeding history.

## **6.2 Methods**

Wedge-tailed Shearwaters were studied at different islands in different years. Pelsaert Island was visited in the 1999/2000 season, but data suffered from intermittent access

given its remote location. Lancelin Island was chosen in 2000/2001 season and Rottnest visited in 2001/2002 to facilitate respirometry.

Hatching was documented to obtain known-age nestlings at Rottnest Island, but less at Lancelin Island (due to injury to the researcher). At Lancelin Island, Wedge-tailed Shearwater nestlings were monitored throughout their ontogeny to obtain 12 h weights and morphometric measurements and frequent weighing was conducted in March. In contrast, known-age nestlings at Rottnest Island were only revisited prior to fledging on 11 April 2002 to conduct a frequent weighing schedule, to measure resting metabolic rates and to monitor the period of weight recession before fledging. During this phase, nestlings often travelled to the entrance of the burrow at night and the use of knock-down barricades was not a reliable indicator of adult behaviour. However, 12 h weight differences were used to estimate adult behaviour, assuming that adult visitation resulted in a meal.

### 6.2.1 Nestling feeding

Frequent weighing of Wedge-tailed Shearwater nestlings occurred over four consecutive nights on Lancelin Island from 11 to 15 March 2001 and on Rottnest Island from 16 to 20 April 2002. Nestlings were weighed at 4 h intervals at 17:30, 21:30, 01:30, 05:30 and 09:30 h WST. The frequent weighing data were analysed as detailed in Chapter 4, however a larger meal size was defined for a larger species.

In 2001, the total overnight food consumed by the nestlings throughout ontogeny was estimated from morning weights, using the regression equation derived from frequent

weighing. This resulted in a real time sequence, which displayed the total food consumed by nestlings from 24 January until the whole colony fledged by May.

At Lancelin Island, Wedge-tailed Shearwater nestlings were weighed twice daily from 24 January to 03 May 2001, at 09:30 h and 17:30 h WST. The birds were visited at 09:30 h WST rather than sunrise (as was the case with the Little Shearwater), because of the need to swim to a moored dinghy and drive it to the island. Sampling did not occur on the following days: 20-23 January, 20 February to 01 March, 10 March, 25-31 March, 01-03 April, and 19-24 April 2001. At Rottnest Island nestlings were weighed daily also. Overnight weight increases between 17:30 h and 9:30 h were used to estimate adult attendance.

### 6.2.2 Supplementary feeding

In 2000, 20 Wedge-tailed Shearwater nestlings were each supplementarily fed 20 g daily of mashed sardines. The slurry was composed of tinned sardines in oil, with the vegetable oil discarded and replaced with tuna oil and then subsequently minced. Nestlings were supplementarily fed from 15 to 22 March 2000, on Pelsaert Island in the southern group of the Houtman Abrolhos Islands, weather permitting at a time when nestlings were growing actively. The 20 fed, and another 20 unfed, nestlings were weighed twice daily and measured three times. Another 40 control nestlings were not weighed or measured, but knock-down barricades were used to monitor adult arrivals at their burrows, as well as at those of the 20 fed and 20 unfed nestlings. Thereafter, post-feeding monitoring extended until 28 March 2000. These birds were again monitored intermittently from 16 to 25 April 2000, when knock-down barricades were no longer useful.



### 6.2.3 Respirometry

Respirometry was used to determine resting metabolic rates of known-age nestlings with known feeding histories, during the pre-fledging period in April 2002. The study was conducted at Rottneest Island where Professor Phillip Withers was able to set up the equipment and protocol. A flow-through respirometry chamber was used to measure water loss, and the consumption and expulsion of respiratory gases (Withers and Williams 1990).

A metabolic rate chamber (40 x 15 cm) was used to accommodate a single shearwater, with the bird and chamber kept within a constant thermal environment, set at 20 °C. Before placing the bird into the dark chamber, not unlike a burrow, the system was calibrated for approximately 15 min. This was necessary as the readings for gases varied between days, and throughout the day with changes in barometric pressure. Therefore, a baseline reading for carbon dioxide and oxygen was obtained, and the water vapour was allowed to drop to an asymptote near zero.

Air was supplied from a dive tank. The flow rate of air through the system was 3 Lh<sup>-1</sup>. Water vapour was removed from the air using a commercial desiccant (Drierite ©) before measuring oxygen (VO<sub>2</sub>; ml O<sub>2</sub>g<sup>-1</sup> h<sup>-1</sup>) and carbon dioxide content (VCO<sub>2</sub>; ml CO<sub>2</sub>g<sup>-1</sup> h<sup>-1</sup>) and total evaporative water loss (TEWL; mg g<sup>-1</sup> h<sup>-1</sup>) using standard flow-through respirometry/hydrometry (Withers and Williams 1990). A respiratory quotient was created to represent resting metabolic rate by dividing CO<sub>2</sub> expulsion by oxygen consumption.

On average, a bird could be processed in 1 h and cloacal body temperature ( $T_b$ ; ° C) was measured immediately after removing the bird from the chamber. The bird was weighed before monitoring took place. After the bird had been removed, the chamber had to be calibrated to obtain a departure baseline reading for the variables. This baseline could also be used as the entry baseline for the next individual. Oxygen, carbon dioxide and water readings were obtained by using visual appraisal of the resultant vapour traces.

The water vapour of the air leaving the chamber indicated water loss by the bird, which might be excretory (alimentary tract, kidneys and salt gland), rather than reflect metabolic activity. Other water loss occurs from the respiratory tract or skin; such evaporative loss often accounts for approximately 50 % of the total water loss and increases with increasing temperature, with panting recognised as an efficient way to regulate body temperature.

Nestlings that had been fed the previous night were difficult to monitor early in the morning as they were inclined to defecate. Consequently, they were usually measured after lunch or after defecating into a newspaper-lined cardboard box that was used to house individuals awaiting measurement. Interestingly, for most nestlings the graphs of the respirometry gases steadied within the first 5-10 minutes, while water vapour took a long time to reach an asymptote. This rapid settling of respirometry rates suggests that even a severe disturbance in the daily routine, such as an introduction into a foreign, but burrow-like environment, did not disturb the birds greatly.

Adults appeared more stressed and more likely to defecate than nestlings. Furthermore, their incessant expulsion of a hypersaline solution from the nostrils (Warham 1996) further compounded the problem of water loss in adults. Often the water vapour reading obtained did not reflect the water loss by the bird, but rather a sum of its water lost and the amount of water evaporating in the chamber from some other source. The respirometry quotients of five adults were also determined for comparison with the metabolic rates of the much larger number of juveniles studied. Respirometry was not conducted elsewhere (i.e. for Little Shearwaters) owing to difficulty of transporting fragile equipment and obtaining refills of dive tanks in more remote locations, such as the Houtman Abrolhos Islands.

## **6.3 Results**

### **6.3.1 Meal sizes**

For nestlings on Lancelin Island and on Rottnest Island, the log of the body size index was not a significant factor determining the log weight loss of a nestling. In both years, the log of the previous weight was of importance for predicting log weight loss on Lancelin Island ( $F_{1,159} = 48.1$ ,  $P = 0.000$ ) and Rottnest Island ( $F_{1,180} = 45.0$ ,  $P = 0.000$ ). In 2002, a gap in weight differences around 100 g may depict the boundary between single and double feeds (Figure 6.1). An average uncorrected meal size was calculated for each sampling period (Table 6.1).

**Figure 6.1** The weight differences (g) over 4 h intervals calculated for Wedge-tailed Shearwater nestlings at Lancelin Island in March 2001 and at Rottnest Island in April 2002.

**Table 6.1** The mean ( $\pm$  S.D.) uncorrected and corrected meal sizes and feeding rates of nestling Wedge-tailed Shearwaters in March 2001 and April 2002.

	Lancelin Island March 2001	Rottnest Island April 2002
Number of meals per night $\pm$ S.D	1.3 $\pm$ 0.09	0.8 $\pm$ 0.08
Uncorrected meal size (g) $\pm$ S.D.	59.4 $\pm$ 3.0	56.9 $\pm$ 3.7
Maximum uncorrected meal size (g)	149.1	154.9
Corrected meal size (g) $\pm$ S.D	77.0 $\pm$ 5.5	45.7 $\pm$ 5.3
Maximum corrected meal size (g)	189.6	156.5
Maintenance meal size (g) $\pm$ S.D	74.3 $\pm$ 0.8	55.4 $\pm$ 3.8

The amount of food needed to maintain zero weight gain differed between the two sampling periods (Figure 6.2). The resultant maintenance meal size was larger (Table 6.1) in March 2001 ( $74.3 \pm 0.8$  g) than in April 2002 ( $55.4 \pm 3.8$  g), albeit monitored at different islands.

The short-term intensive sampling periods showed that nestlings on Lancelin Island in 2001, during their period of maximal growth, were fed more often than nestlings on Rottnest Island in 2002 during the pre-fledging period in April. Indeed, 40 % of nestlings remained unfed during pre-fledging (Table 6.2). However, the sampling in April 2002 coincided with adverse weather conditions arising from Ex-Tropical Cyclone Bonnie. The percentage of nestlings fed fluctuated from 23 % in the first night, to 91 %, then 75 % and then to 35 % during the last night. The effect of weather on provisioning patterns will be discussed later.

**Figure 6.2** The amount of food required to maintain zero weight gain over 24 h for Wedge-tailed Shearwater nestlings in March 2001 on Lancelin Island and April 2002 on Rottnest Island.

**Table 6.2** The provisioning rate recorded for Wedge-tailed Shearwaters during frequent weighing.

Number of meals per night	Frequency (%)	
	Lancelin Island March 2001	Rottnest Island April 2002
0	12 (14)	34 (40)
1	41 (49)	35 (41)
2	25 (30)	15 (18)
3	6 (7)	1 (1)
Total number of intervals monitored	84	85
Number of sample nights	4	3

The uncorrected meal size was strongly related to the corrected meal size (Figure 6.3) for both Lancelin Island ( $r = 0.91$ ) and Rottnest Island ( $r = 0.89$ ). The regression equations for these relationships were used to calculate the total food delivered overnight from morning weights recorded throughout the nestling period.

### 6.3.2 Total overnight food received during growth

In 2001, the total food consumed overnight by Wedge-tailed Shearwater nestlings on Lancelin Island increased with date and body mass, but then dropped prior to fledging (Figure 6.4, Table 6.3). The overall pattern of food delivery matched the average weight of 42 Wedge-tailed Shearwater nestlings on a real time scale (Figure 6.5). Two dips in weight gain occurred, one in early February and one in early/mid March. Both corresponded with the formation of heat troughs along the west coast generated by dissipating tropical cyclones. During such times light NE and N winds prevailed. The approximate times when the heat trough associated with each dissipating tropical cyclone affected local weather conditions were as follows: Tropical Cyclone Abigail on 03-06 February, Tropical Cyclone Walter on 06-11 March and Tropical Cyclone

Alistair on 19-22 April 2001. Sampling did not occur during Tropical Cyclone Alistair.

### 6.3.3 Stable isotope analysis of feathers

Feathers collected from Wedge-tailed Shearwater nestlings at different times in the breeding season indicated that a seasonal shift in diet occurred (Figure 6.6). The protoptile was grown in the egg, from resources sourced by the female in November. The mesoptile, grown in January, differed in composition from the contour feathers collected in March and April. Both types of plumage grown outside the egg were derived from food delivered by both parents. A significant difference was detected between the carbon ratio recorded for nestling plumage grown in March and April ( $t = -5.933$ ,  $P = 0.000$ ). Similarly, a significant difference was recorded for the nitrogen ratios for plumage grown in March and April ( $t = -7.007$ ,  $P = 0.000$ ). This suggests that the food delivered by both adults to the nestling changed over time.

### 6.3.4 Supplementary feeding

In 2000, supplementarily fed nestlings went on to reach significantly higher masses than naturally fed nestlings, once supplementary feeding had ceased ( $t_{22} = 5.79$ ,  $P = 0.000$ ; Figure 6.7). Later, at fledging, this mass gain did not appear to translate into higher fledging weights for supplementarily fed nestlings compared to those fed naturally (Figure 6.7), although fledging masses were not documented for all nestlings owing to access problems. A reduction in weight, recorded for both groups from 19 to 22 March 2000, corresponded to the passage of dissipating Tropical Cyclone Olga. Knock-down barricades revealed that the percentage of burrows visited each night by adults was high in all groups, until a dip between 19 and 22 March 2000 (Figure 6.8), corresponding to the passage of dissipating Tropical Cyclone Olga.



**Figure 6.3** The relationships between the corrected meal size and uncorrected meal size in March 2001 on Lancelin Island and in April 2002 on Rottnest Island.

**Figure 6.4** The mean corrected meal sizes received by 38-41 Wedge-tailed Shearwater nestlings from January to May 2001 at Lancelin Island.

**Table 6.3** The mean weight ( $\pm$  S.D.) of nestlings, mean weight difference (uncorrected meal size) and total overnight food received by nestlings during ten-day blocks on Lancelin Island in the 2000/2001 breeding season.

**Figure 6.5** The mean real time daily weights of 42 Wedge-tailed Shearwater nestlings on Lancelin Island monitored twice daily in 2001.

**Figure 6.6** The stable isotope ratios recorded for feathers grown by Wedge-tailed Shearwater nestlings at different times of the breeding season.

**Figure 6.7** The morning and afternoon weights of supplementarily fed Wedge-tailed Shearwater nestlings and naturally fed nestlings.

**Figure 6.8** The percentage of burrows visited by adult Wedge-tailed Shearwaters in March 2000.

### 6.3.5 Temporal patterns of food delivery

In 2001, on Lancelin Island, the percentage of nestlings fed over a 66-night period fluctuated up to two-fold on successive nights (Figure 6.9). Once again, prolonged periods of reduced provisioning corresponded to the presence of heat troughs. In the period leading up to fledging (late April/early May), the feeding rate decreased markedly (Figure 6.9), as did meal size. Similarly, on Rottnest Island, the percentage of nestlings fed also decreased before fledging (Figure 6.10). A dip in feeding around 15 April 2002 coincided with the approach of Ex-Tropical Cyclone Bonnie. A similar dip in provisioning around 24-28 April 2002 coincided with low wind conditions in the area. At Rottnest Island, during the end of an El Niño year in 2002, 17 nestlings monitored were not fed for the 2 to 14 nights prior to fledging.

In March 2001, most nestlings monitored every 4 h over a four-night period on Lancelin Island were fed between 21:30 and 01:30 h (Figure 6.11). On average, 14.8 % of nestlings were fed before 21:30 h, and 70.5 % before 01:30 h, of which 8.7 % were first meals. Another 33.0 % of nestlings received food before 05:30 h, of which 41.4 % of meals were the first food received that night. Of the total number of meals recorded, 22.1 % were second meals and 1 % third meals. On Rottnest Island, in April 2002, most nestlings were fed between 21:30 and 01:30 h. Thus, 21.8 % of nestlings weighed at 21:30 h had been fed and a further 45.3 % were fed between then and 01:30 h, of which 79.5 % were first meals. In the third time period, from 01:30 h to 05:30 h, on average 17.4 % of nestlings were fed, of which 53.3 % were fed for the first time. On Rottnest Island, 20.5 % of the meals recorded were second feeds.

Although surveys were conducted on different islands, in different years and months similar temporal overnight patterns of provisioning were used.



**Figure 6.9** The percentage of Wedge-tailed Shearwater nestlings fed nightly on Lancelin Island in 2001 (n = 41) and Rottnest Island in 2002 (n = 26).

**Figure 6.10** The frequency distribution of intervals between successive feeds of Wedge-tailed Shearwater nestlings just prior to fledging from Rottnest Island in 2002.

**Figure 6.11** The percentage of 22 Wedge-tailed Shearwater nestlings fed at different times of the night in March 2001 on Lancelin Island, and in April 2002 on Rottnest Island.

### 6.3.6 Respirometry

Respirometry was conducted when nestlings were essentially fully grown, but had not yet developed flight muscles. The nestlings used included those at peak weights (Table 6.4), as well as those undergoing mass recession prior to fledging. Although, 53 trials were conducted, only 23 different individuals were used, with some reused to source birds of varied feeding histories. Eight birds were used once, seven nestlings twice, three nestlings three times, three nestlings four times, and two five times.

**Table 6.4** The weights of adult and nestling Wedge-tailed Shearwaters used for respirometry.

	Weight (g)	
	Nestlings	Adults
Average weight (g) $\pm$ S.D.	397.9 $\pm$ 47.5	362 $\pm$ 28.6
Minimum weight (g)	293	327
Maximum weight (g)	507	388
Sample size	50	5

Nestlings of known feeding history ranged from those fed one night earlier (i.e. the previous night) to one last fed 13 nights earlier (Figure 6.12). No difference in the respiratory quotient was detected between nestlings in relation to their feeding history (days last fed before respirometry) ( $F_{1,48} = 0.008$ ,  $P = 0.931$ ), body weight ( $F_{1,48} = 0.418$ ,  $P = 0.521$ ) and fledging weight ( $F_{1,40} = 0.320$ ,  $P = 0.575$ ). No significant relationship was detected between respiratory quotient and the days remaining until the nestling fledged ( $F_{1,40} = 1.656$ ,  $P = 0.206$ ).

**Figure 6.12** The feeding histories of 22 Wedge-tailed Shearwater nestlings used for respirometry measurements in 50 trials on Rottneest Island in 2002.

A significant relationship was also detected between water loss and bird weight (Figure 6.13), ( $F_{1,46} = 11.073$ ,  $P = 0.002$ ). Feeding history appeared to have no significant influence on water loss ( $F_{1,46} = 3.267$ ,  $P = 0.077$ ), nor did the days until the nestlings fledged ( $F_{1,39} = 3.817$ ,  $P = 0.058$ ), nor fledging weight ( $F_{1,39} = 2.184$ ,  $P = 0.148$ ).

The five respirometry quotients obtained for adults, with an average of  $0.689 \pm 0.145$  (range: 0.467 – 0.868), were lower than those recorded for nestlings, with an average of  $0.816 \pm 0.129$  (Table 6.5). An average water loss of  $2.38 \pm 0.875$  mg/g/h was recorded for nestlings. Water loss was difficult to record for adults, resulting in a low sample size, owing to defecation and nasal discharge, with two individuals averaging  $3.469 \pm 0.035$  mg/g/h. The average body temperature of a nestling ( $37.5 \pm 0.7$  °C) was lower than that recorded for five adults ( $38.2 \pm 0.4$  °C; range = 37.5 to 38.8 °C).

**Table 6.5** The means  $\pm$  S.D. for parameters recorded for Wedge-tailed Shearwater nestlings during respirometry.

	Days to fledge (days)	Fledging weight (g)	Feeding history (days last fed)	Body temperature (°C)	Respiratory quotient	Water loss (mg/g/h)
Average	4.83	364.8	47.66	37.5	0.816	2.38
$\pm$ S.D.	$\pm 3.1$	$\pm 35.03$	$\pm 3.11$	$\pm 0.68$	$\pm 0.129$	$\pm 0.875$
Minimum	1	281	1	36.1	0.567	0.2
Maximum	13	445	13	39.3	1.269	4.57
Sample size	42	42	50	48	50	48

**Figure 6.13** The pattern of total water loss in relation to body weight (g) of Wedge-tailed Shearwater nestlings prior to fledging on Rottnest Island, in 2002.

## 6.4 Discussion

### 6.4.1 Provisioning

Wedge-tailed Shearwaters were studied most intensively at Lancelin Island in the 2000/01 breeding season, during conditions favourable for shearwater reproduction. The total overnight food consumed by nestlings increased until obesity was reached and decreased thereafter. Since the food consumed matched patterns of weight gain, this suggests that input is the crucial factor in the creation of obesity and its regression prior to fledging. During the period close to fledging, nestlings were still visited by adults, albeit at a lower rate than during maximal growth, and presumably these young demanded, received or accepted less food than during the earlier growth phase. This suggests that nestling needs and provisioning rates vary throughout ontogeny. Wedge-tailed Shearwater parents appear, when possible, to meet nestling needs, as documented in a favourable year. This is in keeping with the results obtained for the Little Shearwater in a favourable year.

Wedge-tailed Shearwaters also attempted to feed their nestling regularly, as did the Little Shearwaters. However, prolonged slumps in provisioning by the Wedge-tailed Shearwaters coincided with periods of prolonged low winds, such as those associated with dissipating tropical cyclone Walter, that are common from February to April 2001. Similarly, in 2002 and 2000, a decrease in provisioning coincided with low wind conditions due to dissipating tropical cyclones Bonnie and Olga respectively. This implies that the provisioning schedule used by the summer breeding Wedge-tailed Shearwater may not be as regular as that of the Little Shearwater in winter, owing to low wind conditions, when travel is impaired.



Unfortunately, it is difficult, therefore, to draw direct comparisons, since Wedge-tailed Shearwater were studied on different islands and different times. The studies on Rottneest and Lancelin Islands were conducted on different islands, albeit only 111 km apart. Furthermore, conditions in 1999/2000 and 2000/2001 were suitable for shearwater reproduction, deteriorated in 2001/2002 (Chapter 1), and then declined dramatically before the 2002/2003 breeding season (Table 3.4, Integrated Shearwater Monitoring Program 2002, 2006). However it is possible to draw limited comparisons to the Little Shearwater and to contribute towards the discussion of provisioning in shearwaters.

Overall, Wedge-tailed Shearwaters spent less time ashore at night than Little Shearwaters. Adult Wedge-tailed Shearwaters arrived at the colony later at night than the Little Shearwater (Chapter 4, Figure 4.12), with their nestlings also fed later in the night. Arrival patterns were similar at two different islands, but were recorded in different years and in different months. Generally, Wedge-tailed Shearwaters departed soon after feeding, in keeping with other studies (Nicholson 2002). This may reflect the prevalence of squid in Wedge-tailed Shearwater diet and nocturnal foraging.

Stable isotope analysis indicated a seasonal change in diet in the 2002/03 season. During egg formation females appeared to target a narrow range of prey. This may have been facilitated by being away from the colony during the pre-laying exodus and they are able to target preferred prey. Whilst, when foraging to feed nestlings within a comfortable foraging distance from the colony a broader range of prey is targeted, resulting in an overall lower trophic level. A change in diet was observed during the

breeding season, which may have been a product of foraging around a central location, changes in prey availability, competition with conspecifics for limited resources, possibly changing and increasing needs by nestlings or other factors.

The seasonal change in diet associated with changes in stable isotope composition of material produced at a specific time raise the possibility of differences in the energetic or nutritional value per unit mass of food delivered. Differences in nutritional and energetic values may confound any direct comparison of meal size by mass alone throughout growth. Furthermore, diets may vary not only seasonally, but also between colonies, making it difficult to compare the amount of food accepted by nestlings by mass alone. From an adult perspective, the payload carried may provide some indication of adult effort whilst supporting the nestling. In Western Australia, meal sizes accounted for 19.7 % of adult mass in March. At Montague Island in March 1994 they were 12.5 % of adult mass (Schultz 1994).

Maintenance meal sizes of 50.7 g for February and 46.0 g for March recorded for Wedge-tailed Shearwaters at Montague Island, NSW (Tiller 1998) are smaller than those recorded on the west coast. Nestlings growing up on the west coast were fed more frequently and received larger meals, but this may reflect prevailing oceanographic conditions and subsequent food availability in different years and at different locations. Montague Island is located at the southernmost limit of the breeding range of the Wedge-tailed Shearwater on the east coast of Australia, which may account for the smaller, less frequent meals provided to nestlings. Nonetheless, nestlings at Montague Island attained maximal weights at 191 % of their fledging weight (Tiller 1998), whereas those on the central west coast peaked at a maximum of

only 172 % of fledging weights (Chapter 7) during a favourable year for shearwater reproduction. It is possible that the calorific value of food accessed by Wedge-tailed Shearwaters on the east coast is greater than on the west coast.

During the period of peak weight gain leading to obesity, it can be inferred that the total overnight food consumed was greater than the food needed to maintain zero growth. Thereafter, and until fledging, body mass declined as meal sizes failed to match metabolic needs. During this time it appeared that maintenance needs, meal sizes and provisioning rates decreased. However, nestlings were more physically active and often left the burrow at night around this time. Until this point, nestlings have no need to develop muscles and physical stamina to meet the demands of flight and life at sea. Since, fat weighs less than muscle tissue (Guyton 1991), any transition from an inactive nestling to a fledgling ready for life outside the burrow should be accompanied by an increase in overall weight, rather than the drop observed.

Total overnight food delivery in a favourable year decreased leading up to fledging. On Lancelin Island, in March 2001, 86 % of nestlings received at least one meal each night, whereas on Rottnest Island in April 2002, only 60 % of nestlings were fed. Smaller meals were also recorded prior to fledging on Montague Island (Tiller 1998, Schultz and Klomp 2000a). Although the provisioning rate did not drop with 79 % of nestlings fed in February, 67 % in March, and 84 % in April (Schultz and Klomp 2000a). On Montague Island and in this study, adult attendance was estimated by meal delivery. Since, nestlings have been reported to refuse food (Richdale 1939 cited in Tiller 1998), it is possible that adults were still attending. Indeed, it has been suggested that parents will return until their nestling declines food, whereupon it will

be deserted (Simons 1985). All studies suggest that the classical desertion period characteristic of Short-tailed Shearwaters (Serventy et al. 1971) did not occur in Wedge-tailed Shearwaters. Instead, Wedge-tailed Shearwater nestlings may be partially deserted (Pettit et al. 1984) and desertion patterns may vary between years in accordance with nestling condition.

During the pre-fledging mass recession period, respirometry suggested that the metabolic rates of Wedge-tailed Shearwater nestlings did not alter in relation to feeding history or body mass. This was despite some nestlings remaining unfed for up to 13 nights, which suggests that Wedge-tailed Shearwater nestlings maintained a steady metabolic rate, possibly to ensure their departure. Since, this was recorded during pre-fledging mass recession the same result may not be attained during periods of adverse provisioning. However, it is possible that nestlings of species that frequently experience periods with no food delivery might be expected to drop their resting metabolic rate to conserve energy, but Wedge-tailed Shearwaters at the Western Australian coast may not do so, resulting in weight loss during dissipating tropical lows. Similarly, Wedge-tailed Shearwater nestlings on Montague Island were generally fed frequent small meals, and were observed to lose weight more rapidly than Short-tailed Shearwater nestlings between meals, which are accustomed to periods without food (Schulz 1994).

Interestingly, prior to fledging the body mass of nestlings can be used to predict water loss, with lightweight individuals, closer to fledging, losing more water than heavier birds. This suggests that water loss may play a role in pre-fledging weight loss, rather than any change in metabolic rate related to increased exercise. This is in keeping

with carcass analysis, which has shown that water content dropped before fledging, whilst lipid and lean dry mass remained steady, suggesting that water loss is responsible for the pre-fledging weight recession (Phillips and Hamer 1999, Powell 2004). This implies that nestlings fledge with a lipid buffer that may aid them during their metamorphosis from a dependent youngster to a functional adult.

#### 6.4.2 Supplementary feeding

The very short study of supplementary feeding on Pelsaert Island, during a favourable year for shearwater reproduction, saw supplementarily fed nestlings reaching significantly higher peak masses than unfed nestlings. This suggests that, during peak growth, nestlings accept as much food as available and that parents supply food, regardless of nestling condition, so long as environmental conditions allow. This was also found to be true for Short-tailed Shearwater nestlings that peaked at higher masses and fledged at higher masses when supplementarily fed (Wooller and Bradley unpublished). It has been suggested that nestlings that fledge at higher masses have greater survival rates (Sagar and Horning 1998), but fledging weights of supplementarily fed nestlings were insufficient to comment upon correlations between peak mass and fledging mass.

Knock-down barricades showed that provisioning rates dropped in all treatment groups during the passage of a trough (dissipating Tropical Cyclone Olga), but most noticeably in the supplementarily fed group. This may indicate that Wedge-tailed Shearwater parents can gauge nestling condition and make less effort to feed young in good condition. Adults assessed nestling body condition and fed larger meals to nestlings in poor body condition in both the Cory's Shearwater (Granadeiro et al.

1999) and the Wedge-tailed Shearwater (Baduini 2000). In the current study, a drop in provisioning to well-fed nestlings during adverse conditions would have allowed adults to preserve their own body condition. On the other hand, unsupplemented nestlings were fed at a higher rate than supplemented ones, suggesting that their parents worked harder to protect their investment. Most likely they were able to do so without endangering their own threshold body condition, as suggested by the Little Shearwater results (Chapter 4). After the cessation of adverse conditions, it appears as if the parents of nestlings within the supplementarily fed group were able sustain higher provisioning rates, possibly because other adults were still recovering from their extra effort during the period of adverse weather, which increased travel costs.

#### 6.4.3 Provisioning and weather

In each year, a reduction in food delivery matched adverse weather conditions associated with a dissipating tropical cyclone. This slump was recorded on different islands at different latitudes, ranging from the Houtman Abrolhos to Rottneest Islands. Such periods were associated with low wind conditions that prevailed during the heat trough, and their north-easterly to northerly direction. During such glassy conditions, Wedge-tailed Shearwaters were often observed rafting at sea, suggesting that conditions were not suitable for foraging, or travel to and from the colony. At such a time, adult maintenance needs alone may be covered.

During El Niño years, as well as transition years between El Niño and La Niña conditions, the frequency of tropical cyclones increases (Hamlet and Fisher 1967, Meteorology 1998, Nic Dunlop 2004, pers com, Colls and Whitaker 2001, Integrated Shearwater Monitoring Program 2002, 2006). As a result, more dissipating tropical

cyclones would be expected to travel down the coast. Evidently, each prolonged period of low wind conditions appeared to have predictably adverse effects on Wedge-tailed Shearwater provisioning. The number of such incidents experienced by a cohort is related to climatic conditions and would have implications for breeding success or act in a subtle manner, by causing deviations from an optimal provisioning schedule. Since costs are passed on to the nestling, lower quality nestlings may be produced with reduced post-fledging survival chances. However, during such times only higher quality adults breed, thereby gaining an advantage in terms of life-time reproductive success.

## **7 Chapter 7: Wedge-tailed Shearwater hatching and nestling growth**

### **7.1 Introduction**

This chapter explores the growth of nestlings on Lancelin Island during a favourable year for shearwater reproduction along the Western Australian coast. Wedge-tailed Shearwaters are expected to follow lineage-specific patterns of growth and development characteristics of Procellariiformes. Striking among these is the phase of nestling obesity, during which nestlings attain weights well in excess of adult or fledging weight (Warham 1990) and a plethora of hypotheses have been presented to explain this trend (Warham 1990, Brooke 2004, also see Chapter 1). In this study attention was also paid to growth of plumage. Global growth curves will be created to define growth, which can be compared to a study conducted at a more northern location (Nicholson 2002). Hatching synchrony was determined on Rottneest Island and discussed in terms of resource availability along the Western Australian coast.

### **7.2 Methods**

At Lancelin Island, nestlings were weighed twice each day, weather permitting, at 09:30 and 17:30 h from the termination of the guard period, on 24 January 2001, until fledging. Sampling did not occur on the following days: 20 February to 01 March, 10 March, 25-31 March, 01-03 April, and 19-24 April 2001. Similarly, nestlings were weighed twice daily on Rottneest Island during the pre-fledging period in April 2002. At both sites nestlings were measured at seven-day intervals. Other, details of



methodology followed those described in previous chapters, such as the logistical growth curves created for Little Shearwaters in Chapter 5.

## **7.3 Results**

### **7.3.1 Hatching**

Size differences observed between nestlings, on Pelsaert Island in 2000 and on Lancelin Island in 2001, indicated that Wedge-tailed Shearwater young hatched asynchronously. Hatching asynchrony was documented in 2002, on Rottnest Island, for 35 nestlings (Figure 7.1), which hatched over a period of 17 days. At Rottnest Island, 17 % of nestlings hatched on the median hatching date (19 January 2002) and 40 % hatched, within one day either side of this date, 60 % within two days of the median hatching date, and 74 % within three days either side of this date.

### **7.3.2 Nestling feeding**

On Lancelin Island, the weight gain of 14 known-age Wedge-tailed Shearwater nestlings followed the pattern typical for Procellariiform nestlings. Weight gain was initially rapid and peaked at a weight well above fledging weight (Figure 7.2). In Chapter 6, the average weight of 42 Wedge-tailed Shearwater nestlings, on a real time scale (Figure 6.5), followed a similar pattern, and it was possible to account for the slumps in weight gains evident in Figure 7.2, in terms of adverse weather conditions.

**Figure 7.1** The hatching distributions of 35 Wedge-tailed Shearwater nestlings on Rottneest Island in 2002.

**Figure 7.2** The growth curve of 14 known-age Wedge-tailed Shearwater nestlings on Lancelin Island in 2001 from hatching (day 1) to fledging (day 102).

These adverse conditions are also evident in the individual logistic growth curves of the 14 known-age nestlings. Individual growth curves highlight differences in weight gain between nestlings, display fluctuations of weight gain over time, but also show that each follows a similar overall pattern (Figure 7.3). Global logistic growth curves fitted to the combined morning weights of the 14 known-age Wedge-tailed Shearwater nestlings (Figure 7.4) peaked at an asymptote of  $532.85 \pm 3.310$  g, with a growth rate of  $0.081 \pm 0.002$  and a point of inflection at  $23.04 \pm 0.320$ , with a reasonable fit ( $r^2 = 0.887$ ).

The peak weights of 45 nestlings were documented during different years and at different sites. The average peak weight recorded was  $593.2 \pm 35.9$  g with a range of 505-654 g. For a subset of 38 of these juveniles, their fledging weights were also known, and these individuals peaked at an average of  $592.1 \pm 33.9$  g with a range of 505-635 g. This indicates that a representative subset was used in the subsequent analysis, in which no correlation was detected between peak mass and fledging weight (Pearson's correlation  $r = 0.16$ ,  $P = 0.38$ ,  $n = 38$ ).

For 35 adults, an average weight of  $390.7 \pm 42.6$  g was recorded (range: 310-499 g). The average was used as a comparator, although this value included adults that had fed nestlings and ones still carrying food (Figure 7.5). Based on this, nestling Wedge-tailed Shearwaters peaked, on average, at 158 % of average adult weight and the heaviest nestling represented 167 % of the average adult mass recorded in the study.

**Figure 7.3** Logistic growth curves were fitted to the morning weights obtained for 14 known age Wedge-tailed Shearwater nestlings monitored at Lancelin Island in 2001.

**Figure 7.4** The logistic growth curve fitted to the morning weights of 14 known-age Wedge-tailed Shearwater nestlings on Lancelin Island in 2001 ( $r^2 = 0.887$ ).

**Figure 7.5** The frequency distribution of the weights recorded for 37 adult Wedge-tailed Shearwaters during nestling feeding.

Two Wedge-tailed Shearwater nestlings, one on Lancelin Island and one on Rottnest Island, were known to have been raised by a single parent from hatching, as the partner was found dead in the burrow. Each nestling grew to dimensions similar to those fed by two parents and both fledged, but remained at lower weights throughout development than those with two parents.

Wedge-tailed Shearwater nestlings fledged at an average fledging weight of  $380.5 \pm 31.7$  g, based on the combined data for all years and locations (Table 7.1). The fledging weights on Rottnest Island in 2002 were lower than those for 2000 and 2001 at other breeding locations. A significant difference was detected between the weights recorded at each site in the three different years ( $F_{2,51} = 9.55$ ,  $P = 0.000$ ).

**Table 7.1** Mean ( $\pm$  S.D.) fledging weights (g) of Wedge-tailed Shearwater nestlings with two parents on Pelsaert Island in 2000, Lancelin Island in 2001 and Rottnest Island in 2002.

	Fledging weight (g)			
	All combined	Pelsaert Island	Lancelin Island	Rottnest Island
Average	380.5	386.8	395.3	360.9
S.D.	31.7	25.5	28.2	27.2
Minimum	314	353	352	314
Maximum	441	413	441	422
Sample size	54	5	27	22

The average nestling period documented at Rottnest and Lancelin Island was very similar, both in its mean and range (Table 7.2). No correlation was detected between the nestling periods and fledging weights of 25 nestlings using combined data for Lancelin Island and Rottnest Island (Pearson's correlation coefficient = 0.18). A significant differences in means was detected between the two sites ( $t_{23} = 3.2$ ,  $P = 0.004$ ).



**Table 7.2** The mean ( $\pm$ S.D.) nestling period (days) for Wedge-tailed Shearwater nestlings on Lancelin Island in 2001 and Rottnest Island in 2002.

	Fledging period (days)		
	All combined	Lancelin Island	Rottnest Island
Average	102.5	104.0	101.1
S.D.	2.7	2.5	2.1
Minimum	97	99	97
Maximum	108	108	104
Sample size	25	12	13

### 7.3.3 Morphometric and plumage growth

Individual logistic growth curves were fitted to head length (Figure 7.6), culmen length (Figure 7.7), tarsus length (Figure 7.8), the length of the wing bones (Figure 7.9), the length of the whole wing including primaries (Figure 7.10) and coverts (Figure 7.11). The individual growth curves highlighted individual variations in growth rates and asymptotes reached. Individuals often appeared to have decreased in size, as was especially obvious near the asymptote, despite a single person measuring all nestlings.

Global growth curves were generated for several parameters (Figure 7.12). The tarsus length and wing covert measurements reached an asymptote earliest in nestling life. The growth parameters of the logistic curve that produced the best fit are listed in Table 7.3. A high curve fit was obtained, with coefficients of determination ( $r^2$ ) ranging from 0.96 to 0.98. A good value for  $r^2$  was obtained for wing growth, however the asymptote calculated by the logistic growth curve for wing length greatly exceeds adult dimensions (Tables 7.3 and 7.4). This indicates that the logistic growth curve was not suitable for a parameter with limited number of measurements taken near its asymptote.

**Figure 7.6** The head length (mm) of six known age Wedge-tailed Shearwater in relation to their age (days) since hatching.

**Figure 7.7** The culmen length (mm) of six known age Wedge-tailed Shearwater nestlings in relation to their age (days).

**Figure 7.8** The tarsus length (mm) of six known age Wedge-tailed Shearwater nestlings in relation to their age (days).

**Figure 7.9** The length of the wing bones (mm) of six Wedge-tailed Shearwater nestlings in relation to their age (days).

**Figure 7.10** The wing length (mm) in relation to their age (days) for six Wedge-tailed Shearwater nestlings.

**Figure 7.11** The length of wing coverts (mm) of six Wedge-tailed Shearwater nestlings in relation to their age (days).

**Figure 7.12** Global growth curves for 14 known-age Wedge-tailed Shearwater nestlings on Lancelin Island for different skeletal and plumage measurements.



**Table 7.3** The mean ( $\pm$ S.D.) growth parameters for six linear measurements of 14 known-age Wedge-tailed Shearwater nestlings generated using logistic growth equations in 2000 on Lancelin Island.

\* indicates that the logistic growth curve is not a good model for wing growth, because of the limitations of period in which measurements can be made, despite  $r^2$  being favourable.

Measurement	A Asymptote (mm)	K Instantaneous rate of growth (mm day <sup>-1</sup> )	T Time to inflection at 50% (days)	$r^2$ Coefficient of determination
Head length	84.10 ( $\pm$ 0.30)	0.049 ( $\pm$ 0.001)	1.18 ( $\pm$ 0.35)	0.98
Beak length	37.06 ( $\pm$ 0.21)	0.047 ( $\pm$ 0.002)	3.00 ( $\pm$ 0.49)	0.96
Tarsus length	50.16 ( $\pm$ 0.21)	0.068 ( $\pm$ 0.002)	7.66 ( $\pm$ 0.33)	0.97
Wing length	373.07* ( $\pm$ 14.4)	0.039 ( $\pm$ 0.001)	74.82 ( $\pm$ 2.25)	0.98
Wing bone length	11.04 ( $\pm$ 1.11)	0.059 ( $\pm$ 0.002)	28.79 ( $\pm$ 0.64)	0.96
Covert length	64.52 ( $\pm$ 0.46)	0.200 ( $\pm$ 0.10)	41.78 ( $\pm$ 0.31)	0.97

**Table 7.4** Morphometric measurements of adult Wedge-tailed Shearwaters on Lancelin Island (n = 33) and Rottneest Island (n = 4); data from the two islands were combined.

	Weight (g)	Head bill (mm)	Beak length (mm)	Tarsus (mm)	Wing (mm)	Tail (mm)
Average	390.70	84.7	36.9	49.8	284.9	130.5
S.D.	$\pm$ 42.6	$\pm$ 2.0	$\pm$ 1.6	$\pm$ 1.5	$\pm$ 7.7	$\pm$ 25.2
Minimum	310	79.9	33.4	46.6	263	117
Maximum	499	90	41.2	52.5	298	278
Sample size	37	37	37	37	37	37

Traditionally, only the whole wing is measured. In Figure 7.12 the growth of the wing and wing bone are displayed as separate global growth curves. Both measurements start from a common point, the wrist. A scatter plot was produced which combined the data for both years (Figure 7.13) to highlight the relationship

between skeletal and feather growth within the wing. The wing bones in the wrist stopped growing after approximately 60 days and subsequent elongation of the wing stemmed from the growth of primary feathers.

The growth of individual feathers followed the same pattern as the Little Shearwater. The nestling hatched with protoptile. Later, a thick layer of mesoptile grew and finally the contour feather emerged, engorged in blood and encased in a sheath, progressively drying up, shedding the dry sheath and uncurling as a contour feather. The different feather types emerged from the same follicle and were attached to one another. It was a continuous structure, in which only the structure of the feather varied with phase. The growing contour feather is capped by a layer of mesoptile and, occasionally, still the protoptile. The protoptile wears off before fledging, whilst the mesoptile may be shed. This shedding occurs at a different rate on different parts of the body, and was measured as the percentage of down remaining (Figure 7.14).

The tail mesoptile grew before the tail contour feather (Figure 7.15). Similarly, the mesoptile growth preceded the contour feather grown in scapular tracts (Figure 7.16). These figures serve to document the continuous nature of feather growth throughout ontogeny and the disappearance of the down, as the mesoptile breaks off the tip of the contour feathers. It also shows that the growth of structurally important feathers occurs after nestlings reached an age of 50 days, when contour and flight feathers appear to grow, (Figure 7.13, 7.15 and 7.16). Feathers essential for performance during flight and underwater pursuit, such as primaries and tail feathers grow during this period.

**Figure 7.13** The wing growth of 15 known age Wedge-tailed Shearwater nestlings.

**Figure 7.14** The percentage of down remaining on 15 Wedge-tailed Shearwater nestlings prior to fledging.

**Figure 7.15** Tail growth phases for 15 Wedge-tailed Shearwater nestlings.

**Figure 7.16** The growth of mesoptile and contour feather for 15 Wedge-tailed Shearwater nestlings.

The comparison of nestling growth rates and final asymptotes reached by skeletal measurements of nestlings on Lancelin Island and Varanus Island taken in different years, suggest that differences exist (Table 7.3 and 7.5). This may be a result of oceanographic conditions or latitude. Similarly, adult measurements are smaller at the North-west Shelf than near Perth. At Varanus Island, the mean head length was 78.5 ( $\pm$  2.8) mm, beak length was 34.9 ( $\pm$  1.2) mm, tarsus length was 45.8 ( $\pm$  1.7) and wing length was 273.7 ( $\pm$  10.1) mm for 50 adults (Nicholson 2002), compared with head length was 84.7 ( $\pm$  2.0) mm, beak length was 36.9 ( $\pm$  1.6) mm, tarsus length was 49.8 ( $\pm$  1.5) mm and wing length was 284.9 ( $\pm$  7.7) mm for 37 adults breeding further south. Bergman's rule (Krebs and Davies 1990) predicts that smaller size individuals of a species live in a warmer climate. However, the adaptive advantage of this is unclear to a pelagic seabird.

**Table 7.5** Mean ( $\pm$  S.D.) growth parameters for four linear dimensions for 11 Wedge-tailed Shearwater nestlings in 1998 and 22 nestlings in 2000. T was measured from the first of January, as hatching dates were not known (source: Nicholson 2002).

Year	Measurement	A Asymptote (mm)	K Instantaneous rate of growth (mm day <sup>-1</sup> )	T Time to inflection at 50% (days)	r <sup>2</sup> Coefficient of determination
1998	Head bill	81.7 ( $\pm$ 0.62)	0.052 ( $\pm$ 0.004)	-0.395 ( $\pm$ 1.67)	0.914
2000		82.0 ( $\pm$ 0.23)	0.059 ( $\pm$ 0.002)	-1.434 ( $\pm$ 0.91)	0.963
1998	Beak length	36.44 ( $\pm$ 0.35)	0.058 ( $\pm$ 0.006)	3.68 ( $\pm$ 1.86)	0.851
2000		37.32 ( $\pm$ 0.18)	0.063 ( $\pm$ 0.004)	3.02 ( $\pm$ 1.16)	0.911
1998	Tarsus	49.03 ( $\pm$ 0.27)	0.087 ( $\pm$ 0.007)	7.48 ( $\pm$ 1.22)	0.861
2000		49.28 ( $\pm$ 0.15)	0.109 ( $\pm$ 0.006)	6.68 ( $\pm$ 0.74)	0.906
1998	Wing	346.8 ( $\pm$ 52.1)	0.035 ( $\pm$ 0.003)	72.75 ( $\pm$ 8.80)	0.928
2000		352.1 ( $\pm$ 10.04)	0.04 ( $\pm$ 0.001)	63.49 ( $\pm$ 1.78)	0.983

## 7.4 Discussion

### 7.4.1 Weight gain and hatching

Like most Procellariiform nestlings, Wedge-tailed Shearwater nestlings attained weights well in excess of fledging and adult weights. This has been observed in other studies of the species (Pettit et al. 1984, Schultz 1994, Tiller 1998, Schultz and Klomp 2000a, Baduini 2002). Unfortunately, logistic growth curves cannot display the drop in weight after the asymptote had been reached. This highlights the need for modification of the logistic growth curve to suit Procellariiform weight patterns (Huin and Prince 2000). The raw weights of individuals (Figure 7.3) showed that most nestlings were similarly affected by weather-related slumps in provisioning, as evident from the average weights of known-age nestlings, and the average real time weight (Figure 6.5), but this effect was masked by the use of logistic growth curves. Food delivery in Wedge-tailed Shearwater was interrupted by low wind situations associated with dissipating tropical cyclones, as discussed in Chapter 6.

Wedge-tailed Shearwater young hatched over a period similar in duration to the laying period of 15 days recorded on Montague Island, off the eastern coast of Australia, where 64 % of eggs were laid within three days either side of a central date (Schultz 1994). At Rottnest Island, a hatching period of 17 days was recorded and 74% of nestlings hatched within three days either side of a central date. However, the laying dates for the Wedge-tailed Shearwater on Montague Island did not display a normal distribution, whereas the hatching of the Wedge-tailed Shearwater nestlings on Rottnest Island did approximate such a normal distribution.



This study did not monitor the laying period. The hatching sequences measured are only as a guide to laying sequences, because of the plasticity in the length of the incubation period in shearwaters. Discontinuous incubation is made possible by the tolerance of shearwater eggs to chilling (Warham 1990). At Coffs Harbour, on the east coast of Australia at a similar latitude to Geraldton on the central Western Australian coast, a laying period of 14 days has been recorded (Roberts et al. 1973) and in tropical waters, such as Hawaii, 33 to 24 days (Schallenberger 1973 cited in Warham 1990). It has been suggested that breeding synchrony increases with latitude (Brooke 1990).

Asynchrony in hatching by Wedge-tailed Shearwater colonies at the central west coast suggests that birds have little to gain from synchronous hatching. However, resources off this coast appear to be anything but stable within a year and between years, since within a given breeding season, mass mortalities of nestlings have been documented in Wedge-tailed Shearwaters at the North-west Shelf (Integrated Shearwater Monitoring Program 2002). Therefore, asynchrony may not necessarily be associated with stability. Here, hatching asynchrony may reflect an inability to target peaks of productivity, rather than being an indication of stability.

This suggests that the obesity in this species, one that attempts to regularly feed its nestling, occurs in an environment which lacks predictable and spatially stable upwellings. The previous chapter suggested that nestlings fledge with a lipid reserve that may increase post-fledging survival and that this may be one function of obesity. Single parents have been known to raise a nestling successfully, once in Manx Shearwaters (Davis 1957 cited in Warham 1990), twice in Fulmars *Fulmarus glacialis* (Ollason and Dunnet 1982 cited in Warham 1990) and by one female Wandering

Albatross (Browns and Adams 1984 cited in Warham 1990). In two instances, a lone parent Wedge-tailed Shearwater managed to feed its nestling to a lower maximal weight and the nestling fledged at a lower weight, presumably with a lower post fledging lipid reserve.

The duration of the nestling period recorded in this study, matches values in the published literature. A nestling period of about 14 weeks has been recorded twice (Roberts et al. 1973) and an average of 109 days was recorded for 33 nestlings (Warham 1990). A prolonged period of nestling development would be suitable for a species operating in stable conditions and with an extended duration of resource availability. This only occurs during favourable years on the Western Australian coast.

Fledging weights and duration of the period varied significantly between the years and islands. Fledging weights and nestling periods varied between individuals, but no relationship was detected between the two variables. This implies that there is no benefit in terms of body mass at fledging for nestlings that depart earlier or those that stay longer in the burrow. However, young Manx Shearwaters that fledge early in the season have higher survival chances than ones fledging later (Perrins 1966). This may lead back to the argument of pair quality, with more experienced or higher quality pairs laying earlier and larger eggs, from which larger nestlings are hatched that experience better growth rates and are more likely to survive (Amundsen et al. 1996, Weidinger 1997).

#### 7.4.2 Morphometrics

The pattern of growth documented for Wedge-tailed Shearwater nestlings followed growth patterns typical for other shearwater species (Warham 1990), which has also been observed in Australian studies of the Short-tailed Shearwaters (Saffer et al. 2000); Fleshy-footed Shearwaters (Powell 2000, 2004) and Wedge-tailed Shearwaters (Nicholson 2002), the latter two studied along the Western Australian coast. The tarsi developed most rapidly, beak length less rapidly, with wings developing much more slowly (Warham 1990). The wing bone matured early during development, as did most skeletal measurements, and thereafter only the flight feathers elongated.

The comparison of growth between different tropical species, suggested that Wedge-tailed Shearwater nestlings that grew up in the sheltered environment of the burrow could enjoy a protracted period of development, unlike the surface nesting terns, in which rapid growth in the early stages of development appears universal (Nicholson 2002). A protracted period of development may be aided by the thick, insulating layer of mesoptile, which could ameliorate the heat loss costs associated with being small.

In this study, data for males and females were not analysed separately and it is not always possible to measure all parts of a growth curve. The initial growth phase of most body components begins to develop within the egg and, subsequently, only the later part of the growth curve can be measured, as is the case for the head, culmen, tarsus and even the wing bone. On the other hand, feathers that initiate growth after hatching and that reach an asymptote well before fledging, such as the coverts, produce typical logistic growth curves. However, the tail and wings cannot be

measured repeatedly to an asymptote, as birds fledge and leave the colony. As a result, the asymptote calculated by the growth curve for the wing reached a value exceeding adult dimensions (Table 7.4). This was also observed for the Little Shearwater and in other studies, such as the Fleshy-footed Shearwater (Powell 2000, 2004) and Wedge-tailed Shearwater (Nicholson 2002).

Feather development is a continuous process and occurs throughout ontogeny. The marked delay in the growth and maturation of flight feathers, from 50 days after hatching until fledging may carry an adaptive advantage. In contrast, body down, and later body contour feathers mature early (see coverts and dorsal feather), possibly to aid in thermoregulation and water repulsion. This suggests that flight and tail feathers, of little use in the burrow, essential for flight performance, grow last, to avoid damage and soiling during a prolonged subterranean existence.

It appears as if wing growth becomes an energetic priority later in development, being less affected by periods of poor provisioning than mass (Ricklefs and White 1975). The flight plumage with which the nestling leaves the island is crucial for survival at sea. A first year bird will not be able to forage efficiently unless its flight apparatus is in good condition and will be unable to undertake the energetically expensive process of moulting to replace feathers during subsequent years (Swadde and Witter 1997). Wing exercise is initiated prior to fledging to condition flight muscles (Saffer et al. 2000) and birds are often seen outside the burrow at this time (Warham 1990). This increased physical exercise, which should result in an increase in resting metabolic rate, but does not appear to contribute to the weight loss experienced by nestlings documented prior to fledging (Chapter 6, Figure 6.5).

Nestlings reach obesity at approximately 70 days, coincident with the initial phase of flight feather formation and it is possible that obesity was a by-product of nutrient limitations. Furthermore, during the growth of flight feathers, relatively large shafts are engorged in blood and metabolically active. This could increase heat loss, and the subcutaneous layer of fat may protect nestling core body temperature.

Fault lines have been observed in Wedge-tailed Shearwater and Little Shearwater feathers during all years. Stress appears to result in the growth of an inferior feather with “fault lines” or weak points of lower density and structural integrity. It is possible that feather development may suffer during periods of poor provisioning. Such fault bars have been used as a reliable predictor of fitness in birds of prey (Bortolotti 2002). It may be useful to monitor these in the future.

In the short term, it appeared as if linear growth was less affected by adverse foraging conditions than by the weight of individuals. It has been suggested that skeletal and plumage growth occurs at a heritable, species-specific rate to prepare the nestling for fledging in a given period (Ricklefs 1979). Nonetheless, inter-annual variations in growth rates and asymptotes have been detected, suggesting that the proximal environment has an influence (Weinecke et al. 2000). Similarly, nestling growth parameters varied between years in Wedge-tailed Shearwaters on Varanus Island (Table 7.5) (Nicholson 2002). Nestling grew faster and larger in 2000 than in 1998. 2000 was a favourable year whilst 1998 was a less favourable year, dominated by negative SOI values and cooler offshore waters (Integrated Shearwater Monitoring Program 2003).

It has been suggested that colonies further south may be more buffered against the effects of climatic variations than colonies further north, such as the Houtman Abrolhos Islands and North-west Shelf (Dunlop et al. 2002). As this may account for the southwards expansion of range observed in several tropical species along this coast (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001). Breeding participation of Wedge-tailed Shearwater on Rottnest and Lancelin Island reacted in a similar manner as those breeding at the North-West Shelf (Table 3.4), however the smaller size attained by nestling at the north-west shelf may reflect a decreased ability of adults to meet the needs of the nestling under the prevailing conditions.

## **8 Chapter 8: Little Shearwater observations at sea and a comparison of dive depth and stable isotope analysis of egg membranes to Wedge-tailed Shearwaters.**

### **8.1 Introduction**

Little is known about the behaviour of seabirds at sea, as this is difficult and time consuming to observe. This chapter presents observations of the seabirds at sea, many only anecdotal. In the absence of better information these observations only serve to elucidate the foraging habits of the Little Shearwater, which are poorly understood. This information is important in understanding the energy delivered to the breeding colony.

Seabirds can be extremely difficult to track and observe at sea, so that more indirect methods must normally be employed to gauge their foraging ability. Unfortunately, radio and satellite-tracking, GPS devices and time-depth recorders were beyond the resources of this study and, in any case, too large to be deployed on Little Shearwaters. In this study maximal depth gauges and stable isotope analysis was utilised. Stable isotope analysis (Chapter 2) was used to give an indication of diet during egg membrane formation in the two species (Chapter 3 and 8), changes in diet during nestling feeding (Chapter 6) and to comment on the diet of Wedge-tailed Shearwaters breeding at different locations. Maximum Depth Gauges (MDGs) were deployed to obtain feedback about the maximal dive depth reached by a bird since attachment of the device. MDGs are light-weight, inexpensive and simple devices (Burger and Wilson 1988).

Shearwaters are pelagic and many engage in pursuit diving (Warham 1990, 1996) and their morphology will reflect this lifestyle (Hertel 1999). Wing dimensions reflect not only flight potential in the air, but also underwater (Warham 1990, 1996, Spear and Ainley 1997a, 1997b). Half-folded wings are often used to propel the birds underwater and the legs are used for kicking, especially when submerging and to manoeuvre (Warham 1990). Leg morphology is thought to reflect dive depth (Wood 1993). The dive potential of Little Shearwater has not been investigated. In this study maximum depth gauges will be utilised only to comment upon dive potential. No scientifically robust conclusions besides the maximal depth reached are drawn.

MDGs have been used to record maximal dive depth in other species, including the Sooty Shearwater (Weimerskirch and Sagar 1997), Black-vented Shearwater *Puffinus opisthomelas* (Keitt et al. 2000), Audubon's Shearwater and Wedge-tailed Shearwaters (Burger 2001). Average dive depths are generally less than the maximal dive depth registered by the MDGs. Often, prey can be apprehended using surface seizing and surface diving to shallow depth (Ashmole 1971 cited in Warham 1990), when prey is brought to the surface by marine predators, or when zooplankton and bait-fish move vertically within the water column. It was predicted that the likelihood of encountering an aggregation of prey at a greater depth would increase with time away from the burrow.

Little information is available about the Little Shearwater at sea. Given its southern distribution it was expected that the species would be associated with cooler sea surface temperatures. Cool water exists inshore, between the Abrolhos Islands and



the mainland, whilst offshore areas are influenced by the Leeuwin Current. Planned voyages on fishing vessels were used to search areas potentially used by Little Shearwaters at sea, to see if they are foraging in the cool inshore waters. The behaviour of Little Shearwaters returning and departing from their breeding site was also presented in this chapter. Consequently, most foraging related information is portrayed in this chapter however further inferences about the diet of female Little Shearwaters during egg formation were included in Chapter 3.

## **8.2 Methods**

### **8.2.1 Maximum Depth Gauge (MDG)**

Maximum Depth Gauges recorded only the maximal depth to which a bird submerged. They are extremely simple devices, which rely upon water pressure compressing a known volume of trapped air in a plastic tube in relation to depth. MDGs were used to determine the depth reached by Little Shearwaters in response to prey distribution. The depth is determined by the compression of a trapped volume of air in accordance to changes of pressure with depth. The maximal compression is determined from the ingress of water which eats away a soluble indicator (Burger and Wilson 1988). MDGs were made out of 60 mm PVC tubing (Tygon© size 14, internal diameter: 2 mm). In this study, each 60 mm MDG weighed approximately 1.4 g, representing less than 1 % body mass. The lumen was coated with a soluble indicator powder (icing sugar), cut into lengths and one end was sealed with Araldite® (Hedd et al. 1997, Mougin 2000). The other end remained open to allow the ingress of water.

The MDGs were kept in airtight bags with moisture absorbent crystals until use. In the field, a specific length of an air pocket (or icing sugar coated lumen) was created by trimming the unsealed end. Initially, 100 mm lengths of tubing were used, but seemed too long for the Little Shearwaters as they were shed readily. Good returns were achieved using a 60 mm long air pocket. For the similar sized Audubon's Shearwater maximum depth gauges 70-90 mm long were used, whilst 70-120 mm long MDGs were deployed on Wedge-tailed Shearwaters (Burger 2001).

The MDG was attached with the sealed end sitting between the shoulder blades and the tail end running posteriorly along the spine. The sealed end was attached to several feathers using a cable tie (Hedd et al. 1997) and superglue. Another cable tie was attached to a few feathers along the posterior length of the MDG to keep it central. Initially, MDGs were shed frequently when attached only to feathers. In order to ensure returns, the superglue had to seep through to the down layer next to the skin. Although well attached, at no time did a bird bleed despite the removal of the feathers with depth gauge. As a standard procedure, the potentially plucked patch of skin was sprayed with an antibacterial wound aerosol (Cetrigen®) found to be effective against sea ulcers on humans working long hours on fishing vessels in saline conditions. All birds so treated were opportunistically monitored on subsequent nights. All had lost the purple spray whilst at sea, the area previously carrying the MDG did not look inflamed and their nestlings continued to be fed.

During incubation, adults were banded uniquely and selected birds were fitted with MDGs. Birds incubating were marked using permanent black markers on their white neck. This allowed easy identification of incubating individuals which had not been

at sea using the burrowscope without the daily handling. When an adult returned from sea its faded black mark was registered and the MDGs retrieved. This system minimised repeat handling to identify birds carrying MDG and thereby minimised interference with the egg and incubating adult. During nestling feeding, adults were also fitted with MDGs. In following nights burrows were checked to read or retrieve depth gauges at approximately 21:00 h following a fixed route. It is possible that a bird arrived back at the colony after this time and was located during a future night, however approximately 80 % of burrows had an adult with them at this time (Chapter 2).

The long duration of incubation shifts and long absences during the nestling feeding period increased the likelihood of MDG removal by adults, both in the burrow before departure or at sea. The best returns were achieved if an MDG was attached to an incubating bird with a low body weight, evidently near the end of its incubation shift (i.e. around 155 g) when the opportunity for it to remove the MDG was reduced. Despite such efforts, MDGs were often shed at sea, which made it difficult to obtain depth values for long absences during both incubation and nestling feeding periods.

During nestling feeding, birds were fitted with a maximal depth gauge when a low weight was reached and a departure for a long trip was anticipated. However, this did not necessarily occur during the next day and the bird returned to the colony the next night, these depth gauges were read and provided information about daily foraging trips. The maximal depth gauges were not removed and replaced, based on animal welfare consideration and the difficulty associated with making a depth gauges stay on a bird. To maximise returns, therefore, a repeat measurement technique was used

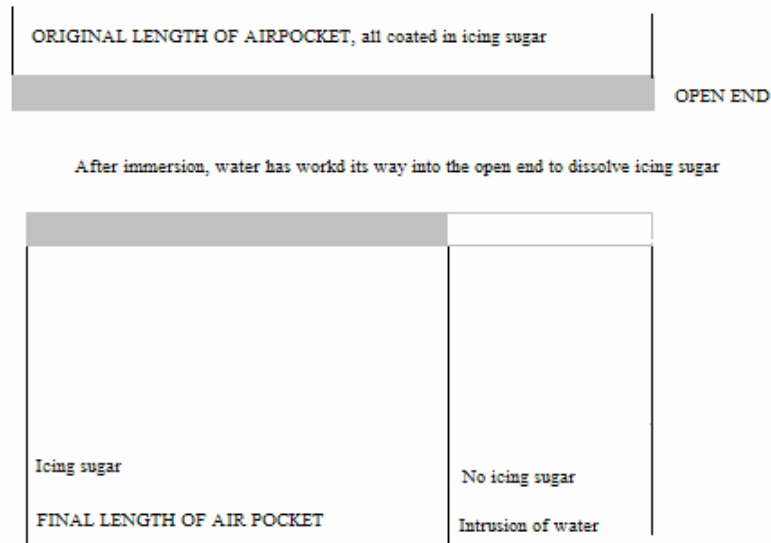
during the nestling feeding period. The MDG was attached in such a manner that the area coated by icing sugar was visible and the original length of the air pocket documented ( $\pm 0.1$  mm) using callipers. Subsequently, the distance eaten away by the encroaching water could be measured ( $\pm 0.1$  mm) using callipers without removing the MDG.

Repeat readings were taken of two depth gauges, instead of removing the MDG at the first reading. On each of the two occasions the depth recorded was greater than previously. The decision to keep the function depth gauge on the bird was made after recording a shallow depth (less than 10 m). Repeat readings retained the potential to gain data from the next long absence (which is difficult to measure) instead of removing after a short absence, as it is difficult to time exactly when birds departed on a long absence and if MDG are not shed at sea.

Returns of gauges after long absences were few, as birds often shed MDG. If an MDG was encountered on a bird after a long absence, it was removed, since the bird had foraged for a prolonged period, whilst carrying a MDG and may have accommodated increased flight costs. Depths attained by adults were calculated using the formula of Burger and Wilson (1988). This formula has been used in other studies to calculate depth (Hedd et al. 1997), nonetheless field trials were conducted to validate its use in this study.

The formula used to calculate maximum depth reached was:

$$\text{Depth (m)} = 10.08 \times ((\text{original air pocket length} / \text{final air pocket length}) - 1)$$



**Figure 8.1** Maximum depth gauges depicting the length of original air pocket, coated in icing sugar prior to immersion in water. The air pocket is compressed with dive depth and water intrudes through the open end dissolving the icing sugar. This leaves behind the final length of air pocket, still coated in icing sugar, which depicts the smallest volume to which the air within the depth gauge has been compressed during successive dives.

The arrival and departure behaviour of adult Little Shearwaters at the colony was monitored while deploying and retrieving depth gauges, appeared to reflect duration of foraging trips (short and long absences) and weather systems as also observed during other aspects of the research. A long absence was characterised by the absence of one bird from the burrow for several days, while the other adult provided intensive care, either in the form of continuous incubation or nearly daily feeding of nestlings.

### 8.2.2 Calibration of MDG to calculate attained depth

MDGs used in this study were calibrated from a supply vessel, the *Island Leader II*. A handline, equipped with non-stretch cord marked at 0.5 m intervals, was used to suspend MDGs to different depths. The MDGs were attached using cable ties with the open end pointing downwards. Heavy weights were attached to the cord to reduce the effect of any current. However, the boat also swung when anchored. Furthermore, the freeboard was high and often seas or swell moved the boat and water in a way that could make it difficult to submerge the MDG to a known depth. To overcome the problem associated with free-board, a ribbon tied to the cord was used to mark the desired depth of submersion, and the MDG was lowered until the ribbon hit the surface of the ocean. The original length of the air pocket on the MDG was recorded, as was its final length after submergence. The resultant ratios (original length to final length of air pocket) obtained at known depths were compared to those calculated from the formula developed by Burger and Wilson (1988).

### 8.2.3 Leg measurements

The tarsometatarsus was measured twice at the midpoint, once to gauge medial-lateral flattening of the leg and a second time to measure its anterior-posterior width. Such a cross-sectional ratio was also used by Wood (1993) as an indication of diving capacity.

## 8.3 Results

### 8.3.1 Calibration of MDG

The ratio of the original air pocket to the air pocket calculated from the formula compared favourably to readings obtained from depth gauges sent to known depths off an anchored vessel (Figure 8.2).

### 8.3.2 Maximal dive depth while incubating and feeding nestlings

A total of 29 MDG readings were obtained (Figure 8.3) from 24 MDGs on 22 different birds. One bird was reused twice during nestling feeding in 2002, for both short and long absences using different MDGs. Another bird carried an MDG in 2002 during incubation, resulting in a long absence, as well as during daily feeding, resulting in short absences unfortunately no long absence was measured for this individual during nestling feeding. In each case, the depths reached by a bird was greater during a long absence, recorded during both incubation and nestling rearing, than after the short (daily) absence recorded during nestling feeding.

In October 2002, during nestling feeding, one MDG was read three times on successive nights and another was read four times (Table 8.1). On each occasion there was an increase in depth. This pattern suggests that the likelihood of a deeper dive increases with time at sea and that individual foraging behaviour is flexible, in response to prey encountered. Furthermore, different birds may meet different conditions at sea, as indicated by the different depths recorded by the two birds (Table 8.1).

**Table 8.1** The depths reached by two Little Shearwaters with increasing durations of absence from their colony.

Individual 1		Individual 2	
Days at sea	Depth (m)	Days at sea	Depth (m)
1	12.4	1	5.0
4	23.7	2	7.0
10	29.2	3	7.2
		11	19.5

During incubation, an average maximal dive depth of 20.8 m was reached. During the nestling feeding period an average maximal dive depth of 28.1 m was recorded during long absences, whilst during short absences an average maximal dive depth of 16 m was reached (Table 8.2, Figure 8.4). Given the small sample size and the repeat measurements conducted on three depth gauges during nestling feeding no statistical analysis was conducted.



**Figure 8.2** Calibration of maximum depth gauges: values obtained at sea by immersing depth gauges to known depths are compared with values calculated from the formula from Burger and Wilson (1988).

**Figure 8.3** The maximum dive depths attained by Little Shearwaters during incubation and nestling feeding during short and long absences.

**Table 8.2** The dive depths (m) reached by adult Little Shearwaters during different phases of parental provisioning.

**Figure 8.4** The maximal depths (m) recorded by gauges in relation to the number of days the number of day a Little Shearwater had been carrying the gauge.

### 8.3.3 Time at sea

During incubation, when only long absences were recorded, an MDG was on a bird for an average period of 8.3 days, similar to the average of 8.6 days recorded for long absences during nestling feeding (Table 8.2). During the nestling feeding period, whilst one adult attended to the nestling on a near daily basis (short absences), the average duration a MDG spent away from the burrow was naturally much less ( $1.5 \pm 1.0$  days). However, this includes repeat readings of MDGs taken 1- 4 days after deployment, where the bird returned to the colony each night during daily provisioning of food for the nestling (Chapter 4). The duration of absence recorded whilst monitoring depth gauges revealed a bimodal distribution (Figure 8.4), which suggests that a bimodal foraging strategy is used by the Little Shearwaters on Beacon Island. Bimodal, in the sense that one adult feeds the nestling nearly daily for a series of nights, while the other adult is absent from the colony for a long period of time.

### 8.3.4 Leg morphology and dive depth

The maximal dive depth recorded by a Little Shearwater off the Western Australian coast was 33.7 m which was reached during a long absence, however during short absences a maximal dive depth of 32 m was recorded. The legs of Little Shearwaters were antero-posteriorly flattened, with a ratio of  $2.3 \pm 0.2$  ( $n = 98$ ) measured between the largest and smallest cross sectional diameters (Table 8.3). This places the Little Shearwater into a category of leg morphology comparable with deep divers, such as the Short-tailed Shearwater (Wood 1993). Measurements obtained for 37 Wedge-tailed Shearwater along the Western Australian coast differed from conspecifics measurements off the eastern coast of Australia, near Wollongong ( $34^{\circ} 25' S, 150^{\circ} 54' E$ ).

**Figure 8.5** The frequency distribution of the length of time (days) Little Shearwaters carried maximum depth gauges during 29 absences from the colony.

**Table 8.3** The tarsometatarsal ratio calculated for six species of *Puffinus* shearwaters. Most values are sourced from Wood (1993), apart from those for the Little Shearwater and Wedge-tailed Shearwater measured in this study. Note that there are two different values for Wedge-tailed Shearwaters.

Species	Ratio $\pm$ S.D	Minimum	Maximum
Wedge-tailed Shearwater Fleshy-Footed Shearwater	1.74 $\pm$ 0.16	1.43	2.07
Wedge-tailed Shearwater (this study)	1.97 $\pm$ 0.14	1.71	2.21
Short-tailed Shearwater	2.11 $\pm$ 0.13	1.84	2.42
Little Shearwater (this study)	2.23 $\pm$ 0.21	1.91	2.64
Sooty Shearwater	2.32 $\pm$ 0.17	1.90	2.70
Fluttering Shearwater	2.49 $\pm$ 0.21	2.20	2.97
	2.72 $\pm$ 0.20	2.30	3.07

### 8.3.5 Egg membrane composition

The stable isotope analysis of egg membranes formed by Little Shearwater females from Beacon Island yield values that were not clumped (Figure 8.6). In contrast, the close grouping of values from egg membranes produced by Wedge-tailed Shearwaters from one island, such as Lancelin Island or Rottneest Island was observed. This suggest that Wedge-tailed Shearwater females originating from a particular colony harvested similar food resources.

**Figure 8.6** The delta-13 carbon and delta-15 nitrogen values of egg membranes from Wedge-tailed Shearwater eggs collected in the 2001/2002 breeding season on Rottneest Island, Lancelin Island, Airlie Island and Serrurier Island, as well as from Little Shearwater eggs collected at Beacon Island in 2002.



### 8.3.6 Little Shearwater observations at sea

Little Shearwaters were not encountered between the Houtman Abrolhos Islands and the mainland during 33 boat trips from Geraldton to the Wallabi Group conducted in between early August to late November over the three years of research. In contrast, Wedge-tailed Shearwaters, Fleshly-footed Shearwaters, Australasian Gannets, Great Skuas, Southern Giant Petrels, Hutton's Shearwaters, Cape Pigeons, Yellow-nosed Albatrosses, White-faced Storm Petrels and Wilson Storm Petrels were all seen during such passages.

Approximately, 50% of return trips from the Wallabi Group occurred via the Easter Group. Here, one Little Shearwater was seen early in the morning, when departing the Easter Group, about 4 km SE of Leo's Island housing a large population of breeding Little Shearwaters. This occurred in mid November 2000, when Little Shearwaters were fledging. Similarly, fishermen have observed Little Shearwaters at or before dawn, flying south and west along the Zeewijk Channel (Craig Culliver 2001, pers. comm.), presumably *en route* to foraging grounds.

In the Wallabi Group, Little Shearwaters were seen returning from the west and northwest of Beacon Island during dusk arrival. Furthermore, Little Shearwaters were seen flying away westwards across the western reef of the Wallabi Group before sunrise, in the spotlight of a crayfishing boat during an opportunistic trip. None were seen before dawn on boats south, east and north of Beacon Island. Two adults were observed at sea at least 18 and 28 km northwest of North Island during the pre-breeding season (14 40 km trips, each sunrise to midday). However, in February,

none were observed north of the A-zone line (Big Bank area) while at sea for three weeks, day and night although, numerous Flesh-footed Shearwaters, some Wedge-tailed Shearwaters, Hutton's Shearwaters, White-faced Storm Petrels and Wilson's Storm Petrels were observed. A similar assemblage of shearwaters was regularly observed feeding inshore near Kalbarri, on the baitfish targeted by Spanish Mackerels *Scomberomorus commerson* at that time of the year. Little Shearwaters were also not observed in the shelf waters to the east or south of the Southern Group during two three-day periods at sea in April 2003, nor near the Turtle Dove Shoal during a three-day period in early February 2002, nor during a three-day period south of Geraldton, between Dongara and the Southern Group, in January 2003. This suggests that inshore, shallow shelf waters are not generally utilised as foraging grounds by the species.

Little Shearwaters were seen at dawn flying west and northwest in the waters west of the islands in May 2001 at the western edge of the Wallabi Group platform (pers. observation). They were also observed by tuna fishermen west of the islands, at distances ranging from 37 km to 370 km west off the mid-west coast, further south (Craig Culliver, pers. comm. 2001 and 2002). In August 2002, numerous single Little Shearwaters were observed flying into light west winds during a 170 km transect at approximately 75 km west of the Houtman Abrolhos Islands, from 29° 30' 113° 00' E to 28° 00' 113° 00' E during 10 h transects over a water depth ranging from 1000 to 3000 m. These were spotted, whilst seeking tuna along this heading. Also numerous Wedge-tailed Shearwaters were seen, as well as mainly juvenile Yellow-nosed Albatross, some Southern Giant Petrels, Cape Pigeons and Great Skuas, the occasional Australasian Gannet, but no terns (Craig Culliver, 2002 pers. comm.).

In 2004, they were not observed to forage on the shelf immediately west of the islands (before the 100 m drop-off) in February and March. In contrast, Wedge-tailed Shearwaters, Bridled Terns, Fairy Terns, Common and Lesser Noddies were frequently seen on the shelf. Foraging assemblages composed of Wedge-tailed Shearwaters, Fairy Terns and noddies, would also target baitfish herded by Yellow-fin Tuna *Thunnus albacares* and Spanish Mackerels in January and February on the reef slopes to the west of the island groups and in areas west of the island inshore of the 100 m contour. Similarly, Little Shearwaters were not seen between the island and the 250 m contour during a one-week period at sea in February 2004, although Hutton's Shearwaters and Wedge-tailed Shearwaters were seen at this time.

When recorded at sea, Little Shearwaters were not observed in groups. No rafts of Little Shearwaters were observed and, if encountered at sea, they were present as single birds or loose aggregations. They were not seen to join the foraging activities of other seabirds targeting schools of pelagic fish near the islands or near the coast. At sea, Little Shearwaters did not scavenge behind boats. In contrast, crayfishing boats were often followed by large numbers of Fleshy-footed Shearwaters (February to June), Wedge-tailed Shearwaters, Wilson's Storm Petrels, Great Skuas, Yellow-nosed Albatrosses and the occasional Streaked Shearwater, White-faced Storm Petrel and Cape Pigeon. Closer to the islands or coast, Pacific Gulls and Silver Gulls joined the boats. Observations from fishing vessels thus appeared to show that Little Shearwaters forage a considerable distance west of the islands over water 1000 m to 3000 m deep, whereas Wedge-tailed Shearwaters were more widely distributed and foraged near land.

Generally, Little Shearwaters were recorded near or at the edge of the shelf, or in waters to the west of the shelf. They were observed in the deeper shelf waters to the north-west of the Abrolhos Islands, but not to the east, in inshore, shallow, cooler shelf water. Fishermen also observed Little Shearwaters near edge of the shelf or in deeper water to the west of the shelf south of the islands. Overall, opportunistic observations suggest that the Little Shearwater does not forage inshore, and appears to target deeper water near the edge of the shelf or off the edge of the shelf. The relatively warm, tropical Leeuwin Current follows the shelf.

#### 8.3.7 Arrival and departure patterns

Little Shearwaters observed from a lookout with 360° uninterrupted view regularly approached Beacon Island from the west and north-west. They were not observed to raft in the nearby waters. Nor were they seen flying before dusk in the nearby waters, such as Goss's Passage, by an observer with binoculars in a dinghy, as often was the case for Wedge-tailed Shearwaters and White-faced Storm Petrels. Little Shearwaters did not arrive in large flocks, but rather appeared as a stream of individuals in the twilight. On some nights, more adults appeared to arrive than on others, both in the incubation and nestling period, this is examined later (Chapters 3 and 4).

After circling a section of the island for several turns, often calling in flight, Little Shearwaters landed heavily on the ground often a few meters from the burrow. Birds then scurried towards their burrow and nestling. Birds in flight often collided with buildings especially those with exterior lights or illuminated windows, dropped to the ground and remained sitting, while recovering. Unlike the Wedge-tailed Shearwaters

on Lancelin Island and Rottnest Island, Little Shearwaters often remained in their burrow for most of the night, next to the nestling. On windless nights, an adult would often venture outside the burrow to call, duet and rest in bushes near the burrow. It appeared as if there were arenas in which the birds frequently congregated to call and gather in loose aggregations.

Little Shearwaters departed *en masse* just before dawn, with a large chorus audible on favourable nights before departure. On most mornings, a pre-dawn chorus was heard until civil dawn, becoming silent about an hour before the sunrise. The colony was very vocal on windless days and silent when windy. However, areas protected from the wind, as for example by buildings, were more likely to continue to record calling, even during a windy night. Nightly fluctuations in the dawn and dusk chorus were examined in Chapter 3 and 4.

Some Little Shearwaters launched themselves from the ground, but many climbed through the branches to launch themselves off bushes, especially during low wind conditions. Take-off usually occurred to the east, possibly because the prevailing winds in the morning are dominated by easterly, south-easterly and southerly components. Birds called from the air and ground before taking off. Often, those that departed, while it was still dark, circled over the island; later, when it was lighter, they flew off straight over the water, without turning back. Variability in the call and flight activity of Little Shearwater at dawn and dusk will be examined in Chapter 3 and 4.

Little Shearwaters would arrive about half an hour after sunset and continued to arrive until well after midnight. In 2000, 25 to 27 burrows were monitored for three nights prior to frequent weighing to establish the best time for the first weighing session. On average,  $82.5 \pm 4.1$  % of the nestlings had an adult with them by 20:30 h, whilst at 19:30 h the average attendance was only  $57.4 \pm 6.7$  % (Figure 2.1), whilst prior to sunset all nestling had been unattended by adults. Arrival of adults at night is further investigated in Chapter 4 (Figure 4.12). In mid August, sunset is at 18:00 h and sunrise at 06:50 h, whilst in mid September sunset is approximately at 18:20 h and sunrise at 6:10 h.

## 8.4 Discussion

### 8.4.1 Congruence of theoretical foraging distances with observations

Little Shearwaters arrived from dusk to well after midnight and departed from half an hour before civil twilight until an hour before the actual sunrise. Arrival of adults at night was depicted in Figure 2.1 and Figure 5.12 which suggests that most adults arrive before 21:30h. A similarly persistent nocturnal presence of adults was also noted on Eclipse Island (Warham 1955) and Lord Howe Island (Priddel et al. 2003). This implies that parents engaged in daily provisioning do not forage at night. The maximum time spent at sea by a bird returning daily to the colony with food would thus be 12 - 20 h. Using published flight speeds (Alerstom *et. al* 1993 cited in Warham 1996), a theoretical flight range was calculated, which did not allow for time to forage. When travelling at a flight speed of  $10 \text{ m.s}^{-1}$ , the daily foraging distance from the colony would therefore range from 72 to 120 km. If flying at a maximum

speed of  $14 \text{ m.s}^{-1}$ , a range of 101- 168 km results. Little Shearwaters were seen approximately 75 km west of the islands, over waters 1000-3000 m deep in late August 2002. Here, large numbers of single Little Shearwaters were observed, spread over large areas, but not in flocks (Craig Culliver, 2001 pers. comm.). These observations are consistent with the estimated daily flight ranges.

Large areas west of the islands are rarely surveyed and the feedback received from fishermen skilled in bird identification was valuable. In October 2000, Little Shearwaters were observed 372 km off the coast, at the same latitude as Lancelin Island, where the species breeds (Craig Culliver, 2001 pers. comm.). These may be non breeders or adults engaged in long absences from the colony. Observation at sea during frequent passages to and from the islands showed that Little Shearwaters did not forage between the islands and the mainland. This suggests Little Shearwaters did not seek the cooler inshore waters. The only sightings were near the islands whilst birds commute from breeding to foraging sites.

#### 8.4.2 Location of foraging sites

Little Shearwater behaviour at sea suggests that they dispersed over large areas west of the Abrolhos islands, beyond the continental shelf, over water columns from 1000-3000 m deep. Observations from fishermen were similar to previously unpublished observations by bird researchers on board the CSIRO research vessel the “Franklin”, who recorded Little Shearwaters at sea during the breeding season (Dunlop and Surman unpublished). On 15 September 1996, around 07:45 h, one Little Shearwater was seen west of the Southern Group at  $29^{\circ} 20' 66'' \text{ S}$ ,  $113^{\circ} 35' 62'' \text{ E}$  over water 2175 m deep. Here the SST was  $21.4^{\circ} \text{C}$  and salinity 35.40 ppm. The bird was

observed near some Brown Noddies, Wedge-tailed Shearwaters and Lesser Noddies. Another Little Shearwater was recorded at 07:20 h, further south and west, near some Brown Noddies, Lesser Noddies and Wedge-tailed Shearwaters. Similarly, at 29° 02'49'' S, 113° 19'36'' E, two Little Shearwaters were seen over 2438 m at 09:00 h near some Wedge-tailed Shearwaters, Brown Noddies, Yellow-nosed Albatross, White-faced Storm Petrels and Lesser Noddies. The depths and locations of Little Shearwater sightings indicate that the species forages in deep water far west of the central west coast, in areas where eddies of the Leeuwin Current might be expected to influence oceanography, and not in the cooler, inshore waters as predicted by their distribution. This is in keeping with the distances covered during daily foraging trips (70–170 km depending on flight speed and energy expenditure). However, during prolonged absences, the Little Shearwaters may seek cooler waters potentially a long distance away from the breeding location, which may provide essential energy necessary to maintain reproduction of this colonial species at relatively low latitude.

#### 8.4.3 Maximal dive depth

The depths attained by Maximum Depth Gauges directly calibrated at sea compared well to the depths calculated from a formula. At shallow depths, MDG readings deviated somewhat from the true readings, but MDGs are known to be less reliable for shallow dives (Hedd et al. 1997).

A maximal dive depth of 34 m was reached by a Little Shearwater weighing 171 g after it had fed the nestling. The Black-vented Shearwater weighing 406 g reached a depth of 52 m (Keitt 2003). This result is close to the maximal depth of 57 m for Black-vented Shearwaters, calculated using the allometric equation for maximal dive



depth calculated for penguins  $D_{\max} = 75.95 M^{0.316}$ , where M is mass in kg (Burgers 1991 cited in Keitt *et al.* 2000). For a Sooty Shearwater, weighing 850 g, a maximal dive depth of 67 m was recorded in the field, while the allometric equation predicted a depth of 72 m. For Little Shearwaters a maximal dive depth of 43 m was estimated using the equation. This suggests that Little Shearwaters in this study did not need to operate at their maximal dive depth.

The allometric equation for maximal dive depth for penguins uses average adult weights. These are difficult to define and fluctuate greatly, for example, when carrying extra mass to feed nestlings (Chapter 4). If the weight of a Little Shearwater carrying food was used, at 200 g a maximal dive depth of 45 m results. For Wedge-tailed Shearwaters, at 361 g, the calculated maximal depth of 56.4 m is less than the observed maximal dive depth of 66 m (Burger 2001). This suggests that the equation may not truly reflect a shearwater's dive potential, considering that its morphology is also suited to flight, whereas penguins forage purely underwater.

The dive depths recorded for Little Shearwaters are consistent with those predicted using the relationship between leg morphology and dive depth (Wood 1993). For Audubon's Shearwater, a small bird with short wings, similar to the Little Shearwater, a mean maximum depth of  $15 \pm 12$  m has been recorded that ranged from 6 to 35 m ( $n = 7$ ). Audubon's Shearwaters normally feed within 10 m of the surface (Burger 2001).

The leg morphology recorded for the Wedge-tailed Shearwater in this study differs from results obtained by Wood (1993). Nonetheless, both studies placed the Wedge-

tailed Shearwater at one end of the spectrum, indicative of shallow dive potential. For 19 Wedge-tailed Shearwaters at Hawaii, a mean maximum depth of  $14 \pm 23$  m has been recorded, with a range from 1- 66 m, although most Wedge-tailed Shearwaters fed within 20 m of the surface (Burger 2001). The maximal dive depth of 66 m does not match predictions based on lateral compression of the tarsus (Table 8.3).

Similarly, this maximal dive depth for a species with low wing loading greatly exceeds expectations for a buoyant, broad-winged, tropical species (Warham 1996). Given that the dive depth recorded for the narrow winged Little Shearwater did not exceed that recorded for the broad winged Wedge-tailed Shearwater it is likely that the buoyancy expected to be associated with broad wings does not appear to compromise dive potential. However, at the Western Australian coast conditions may not have presented itself to elicit maximal possible dives from the Little Shearwater.

Surface seizing is often used by shearwaters when prey is accessible and may be less costly in energetic terms than deep diving (Warham 1996, Brooke 2004). This suggests that maximal depth gauges can be misleading and only define a species potential in response to the distribution of evasive prey at the foraging sites accessed.

For example, Wedge-tailed Shearwaters breeding on Montague Island only need to dive to an average depth of 4.1 m and a maximal depth of 6.7 m (Bester 1997).

Similarly, for the Short-tailed Shearwater, an average depth of 10.7 m and maximal depth of 12.9 m were recorded for individuals from Montague Island (Bester 1997), well below dive potential predictions based upon morphometrics. Nonetheless, species appeared to reduce competition by targeting different sections of the water column, in keeping with predictions. This suggests that food availability will influence the need to dive deep. Furthermore, such latent potential may allow

shearwaters in tropical locations occasionally to fill a niche similar to pursuit divers in cold waters and reach prey inaccessible to other seabirds in tropical assemblages (Burger 2001).

During the retrieval and deployment of depth gauges, adults appeared to be using a bimodal foraging strategy to feed the nestling. One parent would return daily to the colony to provide for the dependent nestling, while the other parent was not encountered for a long period of time. The bimodal foraging strategy was further investigated in Chapter 4, whilst potential patterns governing the arrival at and departure from the colony by adult shearwater are monitored in Chapters 3 and 4.

A significant difference in mean maximal depths after short and long absences was recorded. However, no significant relationship between time absent from the colony and dive depth was detected. Furthermore, one of the deepest dives was recorded during a short absence. This suggests that prey distribution, determines dive depth, rather than differences in foraging behaviour during short and long absences.

Similarly, individual variations in dive depth suggest that adult Little Shearwaters are able to adjust their foraging behaviour to suit conditions.

Direct comparison of the time spent at sea during incubation suggests that MDGs may slightly inhibit foraging. In 2002, during incubation, seven birds that carried MDGs had an average duration of absence of  $8.3 \pm 1.1$  days, whereas 25 incubation shifts of birds not carrying MDGs averaged  $7.7 \pm 1.5$  days (Chapter 8). This difference cannot be attributed to lack of vigilance in monitoring burrows, because all burrows were monitored using a burrowscope daily and attending birds had been marked using

waterproof marker. Nonetheless, no differences in adult weights were detected during nestling feeding. This suggests that parents facing increased demands incurred by carrying a MDG ameliorate this by spending more time foraging, rather than compromising adult body condition.

#### 8.4.4 Stable isotope analysis of egg membranes

Little Shearwater females originating from one colony did not appear to target similar resources or trophic levels during egg formation, whilst Wedge-tailed Shearwater females originating from colonies with sufficiently large sample sizes (Rottnest and Lancelin Islands) appeared to target similar food resources or trophic levels. At Rottnest Island, Wedge-tailed Shearwater females engage in a pre-laying exodus (Garkaklis et al 1998). During this prolonged absence from the colony foraging is no longer limited to a central location, which may allow them to seek preferred prey.

Based upon a relatively large sample size of female Wedge-tailed shearwaters at two colonies (Rottnest Island:  $n=12$ , Lancelin Island:  $n=7$ ) they were found to targeted similar resources during egg membrane formation. This may reflect absence of foraging constraints during the pre-laying exodus, during which they may be able to target preferred prey. Conversely, an assumption was made that females from a colony act as a unit, which was used to interpret low sample sizes from egg membranes collected at the North-West Shelf. Based on this assumption, it is possible that females from Serrurier Islands ( $n=1$ ) may target similar resources and trophic level to birds at Rottnest and Varanus Island. Whilst females from colonies on Varanus Island ( $n=3$ ) and Airlie Island ( $n=2$ ) appeared to target different resources at potentially different locations. This may reflect foraging at shallow water locations

of the North-West Shelf, whilst birds from Rottnest Island, Lancelin Island and Serrurier Island may forage in deeper, offshore waters. Therefore the technique gave an indication of foraging behaviour of birds engaged in the same phase of the annual breeding cycle at different locations along the Western Australian coast.

In contrast, Little Shearwater females from Beacon Island did not appear to forage target similar resources during egg membrane formation. It is not known if the females engage in a pre-laying exodus and therefore have the ability to forage unconstrained. Stable isotope analysis of egg membranes suggested that Wedge-tailed Shearwaters fed at a higher trophic level than most Little Shearwaters during egg formation (Figure 8.6). Nonetheless, as indicated by outliers, a few Little Shearwaters did feed at this higher trophic level. Mostly, Little Shearwaters appeared to forage at a trophic level similar to that represented by bait-fish, such as the Scaly Mackerel *Sardinella lemuru* purse-seined off the central coast (Figure 3.3). Stable isotope analysis of egg membranes suggested that Wedge-tailed Shearwaters fed at a higher trophic level than most Little Shearwaters during egg formation (Figure 8.6). Nonetheless, as indicated by outliers, a few Little Shearwaters did feed at this higher trophic level. It is not known if the whole Little Shearwater colony engages in a pre-laying exodus, and may therefore not be able to engage in unconstrained foraging, alternatively egg membrane composition reflects variable food availability during the protracted laying period.

In Wedge-tailed Shearwaters, a shift in food resources targeted during nestling feeding was observed, with a decrease in trophic level being evident (Figure 6.6). This may reflect the constraints imposed by a foraging from a central location whilst

regularly returning to the colony to feed the dependent nestling whose needs increase with size. It is possible that adults target a more diverse range of prey and are therefore less selective whilst foraging is constrained. Here, scavenging on bait such as North Sea Herring discarded by the Western Rock Lobster Industry cannot be excluded (Dunlop and Asmussen unpublished). Stable isotope analysis was able to detect seasonal changes in diet, differences between locations and species. The technique has the potential to contribute insight into otherwise difficult to observe behaviours. Ability to interpret data will increase once reference libraries of prey and predators have been established to comment on ecosystem dynamics and locations.

## **9 Chapter 9: Synthesis - A summary of results and a model of parental provisioning in shearwaters**

Parental provisioning was investigated in two congeneric shearwater species during a favourable year (2000), a transition year (2001) and a less favourable year (2002) for seabird reproduction of the Western Australian coast (Chapter 1), as indicated by previous and ongoing seabird research (Wooller et al. 1991, Integrated Shearwater Monitoring Program 2000, 2001, Surman 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, Surman et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006). This chapter aims to summarise key results distributed throughout the thesis and the key objectives addressed by the study. Foraging and associated constraints of the energy input system to colonies breeding at a central location are discussed. Indirect techniques trailed are evaluated, including the application of stable isotope analysis. A model of parental provisioning for shearwaters is discussed, based on an adult state-dependent regulatory mechanism, which would allow the K-strategists to persist in the highly unpredictable and unstable environment. Suggestions for future research are made to further explore the tentative model. The implications of this potential model on nestling viability are discussed and viewed within the context of climate change.

### **9.1 Summary of key findings**

The two, congeneric species and their characteristics, gleaned from the literature (Chapter 1), together with some findings from this study have been collated in Table 9.1 and Table 9.2. Findings of this study relevant to parental provisioning are

summarised in Tables 9.3 and 9.4. Table 9.5 comments how broad outcomes of the study addressed the objectives introduced in Chapter 1. A tentative model of parental provisioning will be discussed later.

**Table 9.1** A comparison of selected characteristics of the two species of shearwaters studied (Glauert 1946, Serventy et al. 1971, Marchant and Higgins 1990, Warham 1990, 1996, Spear and Ainley 1997a, 1997b).

Attribute	Little Shearwater <i>P. assimilis</i>	Wedge-tailed Shearwater <i>P. pacificus</i>
Adult weight (g) from literature	142-201 195 (15)	300-570 369 (100) 385 ± 38
Body length (cm)	25-30	38-46
Wing span (cm)	58-67	97-105
Wing shape	Narrow wings	Broad wing, large tail
Wing loading (N.m <sup>-2</sup> )	High	Low: 36.8, 29.3, 36 ± 3
Aspect ratio	High	Low: 8.9, 10.3 ± 0.5
Flight style	Flapping flight Flap-glide	Dynamic soaring Glide-flap
Ground speed (ms <sup>-1</sup> )	10.7-14.0	7.7 – 12.6
Suited for low winds	Less so	Better suited
Distribution	Sub-polar temperate to subtropical winters	Tropical, subtropical and temperate summers
Sea-surface temperature	Possibly cool waters	Warm waters
Seasonality	Present at colony most of the year (March to November) Absent over summer (Eclipse Island)	Non-migratory, but absent from colony outside the breeding season
Breeding season	Austral winter Lay: July Hatch: August to September Fledge: October/November	Austral summer Lay: November Hatch: January Fledge: April/May
Egg weight at laying (g)	34 calculated in this study	60 (27)
Egg size (mm)	52.3 x 35.6 this study	64.1 x 41
Egg volume index (LB <sup>2</sup> )	67 (17) this study	114 (36)
Incubation period (days)	52-58 54 (4)	52-54 52.4 (17)
Fledging period (days)	70-75 this study 72 (3)	102 this study 109 (33)



**Table 9.2** Foraging attributes of the two shearwater species are summarised. Indicated in square brackets are values from a parallel study of the Wedge-tailed Shearwater along the Western Australian coast by Dr L.W. Nicholson 2002.

Attributes	Little Shearwater <i>P. assimilis</i>	Wedge-tailed Shearwater <i>P. pacificus</i>
Foraging strategy	Bimodal and co-ordinated (Booth et al. 2000b)	Unimodal (Baduini et al. 2002) or bimodal (Congdon et al. 2003)
Oil in Stomach content	Low	Low
Squid in diet	Mostly fish slurry. No squid observed in this study, but present in other studies, including Abrolhos Islands.	Yes Extensively observed in <i>this</i> study.
Time spent on the breeding island	Long visits: Arrived early and stayed until dawn (also Priddel et al. 2003)	Brief visits: Arrived later in the night, departed soon after feeding [9.5- 11.5 minutes]
Estimated distance to foraging site during short trips (km)	Not seen near island Seen 34 km away	Seen foraging in waters nearby within 20 km and further (also Nicholson 2002)
Estimated range (km)	72- 120 (at 10 ms <sup>-1</sup> ) 101 –168 (at 14 ms <sup>-1</sup> )	40-120 (Integrated Shearwater Monitoring Program 2003)
Maximum dive depth (m)	Not observed at sea. 34 m returns from MDGs	Observed surface feeding, less than 4 m deep Reported maximum: 66 m (Burger 2001)
Tarsal flattening index (maximum diameter/minimum diameter)	2.3	1.8
Follow fishing boats	No	Yes
Scavenge bait from boats	No	Yes, can be hooked by wetliners and longliners
Feeds in flocks	Not observed	Observed
Feeds in aggregations with other species	Not observed	Yes; Fleishy-footed Shearwater, White-faced Storm Petrel, Yellow-nosed Albatross

**Table 9.3** The behaviour of adult Little Shearwaters and Wedge-tailed Shearwaters during incubation and nestling feeding in Western Australia.

Attributes	Little Shearwater <i>P. assimilis</i>	Wedge-tailed Shearwater <i>P. pacificus</i>
From this study		
Mean adult weight (g)		
Pre-laying	170.8 (n = 234)	
Incubation	173.6 ± 17.9 (n = 197)	
Nestling feeding	168 ± 14.8 (n = 569)	390.7 ± 42.6 (n = 37)
Total range recorded (g)	133-217	310-499
Mean duration of incubation shift (days) in 2002	7.5 ± 1.4 (range: 5-11)	
MDG birds in 2002	8.3 ± 1.1 (carrying MDG)	
Incubation trip duration (days) in 2002	7.7 ± 1.4	
Range (days)	5-12	
Weight loss (g per day) during incubation	5.8 ± 1.4 or 3 % of adult weight	
Dive depth during incubation (m)	20.8 ± 3.3	
Range (m)	17.9 – 27.1	
Foraging strategy	Co-ordinated bimodal	
Duration of long absence (days)		
Favourable year 2000	5.9 ± 1.5	
Adverse year 2002	8.9 ± 1.9 (carrying MDG)	
Weight loss (g per day) during daily nestling feeding	5.0 ± 2.5 or 3 % of adult weight	
Average maximal dive depth during daily provisioning (m)	28.1 ± 5.0	
Range (m)	19.5 – 33.7	
Average maximal dive depth during long absences (m)	16.0 ± 7.6	
Range (m)	5 – 32	

**Table 9.4** Parental provisioning by Little Shearwaters and Wedge-tailed Shearwaters. Indicated in square brackets are values from a parallel study of the Wedge-tailed Shearwater at the North-West Shelf by Dr L.W. Nicholson (2002).

Attributes	Little Shearwater <i>P. assimilis tunneyi</i>	Wedge-tailed Shearwater <i>P. pacificus</i>
Mean adult weight (g) used for comparison	170.8 (n = 234) using pre-laying weights	390.7
Range (g)	133-217	310-499
Average fledgling period (days)	71 72 (Warham 1990)	102
Range (days)	68-74 70-75 (Glauert 1946)	97-108
Maximum weight of nestling (g) As percent of adult weight As percent of fledging weight	289 169 % 160%	654 162 % 172 %
Mean fledgling weight (g) As percent of adult weight Range (g) As percent of adult weight	180 105 % 152-218 89 – 128 %	380 97 % 314- 441 87 – 122 %
Feeding frequency (Number of meals per day)	0.89-1.1	0.8-1.3 [1.4, 1.32, 0.96]
Percentage fed each night At maximal growth  Prior to fledging	90 (in 2000), 75 (in 2001) 91 (in 2002)	86  60
Size of meals during ontogeny	Variable	Variable
Corrected meal size (g): Mid max. growth Near fledging As percent of adult weight	29.2-32.2 — 15.8 –20.8 %	77 45.7 [41.8] 11.5-19.7 %
Maximum corrected meal size (g)	52 - 91	156.5-189.6
Maintenance meal size (g): Mid max. growth Near fledging As percent of adult weight	24-32.8 — 14 – 19.2 %	74.3 55.4 14.2 - 18.8 %
Egg weight (g) As percent of adult weight	34 19.9 %	76.9 (Warham 1990) 19.7 %
Average weight of hatchling (g) As percent of adult weight	21 12.5 %	35 12.3 %

**Table 9.5** The objectives and outcomes of this study.

Focus	Objectives	Outcomes
Little Shearwater incubation behaviour	Monitor adult Little Shearwater weights during incubation and durations of incubation shifts.	Individual threshold adult weights seem to influence duration of incubation shifts and absences from colony
Hatching patterns	Should be asynchronous as resources do not exhibit the predicably seasonal shut down characteristic of high latitudes.	Fairly asynchronous: Little Shearwater, whilst Wedge-tailed Shearwater appeared to be more synchronised.
Guard behaviour	Do Little Shearwaters attend to nestlings after hatching?	Nestlings are attended after hatching.
Provisioning of food	Monitor food delivery: meal sizes and patterns of food delivery (frequent weighing and daily weighing).	In both species meal sizes change with age of nestling and nestling were fed near daily.
Provisioning of food	Examine shearwater provisioning under variable conditions within a year and between different years.	Both species fed nestlings nearly daily, however provisioning differed between years and within a year.
Obesity	Should not overfeed: 1. Regular visits/feedback on nestling condition, 2. No migration	Both species overfed nestlings
Obesity	May need a fat buffer in an unstable environment in terms of oceanographic conditions and weather patterns.	Insufficient data to comment on status of whole colony. Proportion of pairs able to reach obesity may vary.
Obesity	Wedge-tailed Shearwaters respirometry indicates water loss prior to fledging.	Loose water, therefore may need lipid as post fledging buffer.
Desertion	Should not desert, no migration.	Lower attendance of nestlings prior to fledging
Pre-fledging weight loss	Examine changes in the basal metabolic rate in Wedge-tailed shearwater nestling using respirometry	Weight loss observed in both species. No change in metabolic rate, but a loss of water was recorded
Mechanism of nestling provisioning – Little Shearwater	Little Shearwater were expected to forage near colony as feed nestling regularly.	Bimodal strategy: long absences and short absences. Co-ordinated absences of adults to create near daily nestling feeding. Co-ordination of parental care deteriorates as oceanographic conditions deteriorate
Mechanism of nestling provisioning	Supplementarily feeding of Wedge-tailed Shearwater nestlings.	Adults reduced provisioning to supplementarily fed nestling during adverse weather conditions, therefore adults are able to gauge body condition and adjust input.

**Table 9.5** – Continued. The objectives and outcomes of this study

Focus	Objectives	Outcomes
Mechanism of nestling provisioning	Examine more subtle mechanism of why shearwaters struggle to reproduce during adverse oceanographic or climatic conditions. This would elucidate mechanism leading to decreased breeding participation or success.	Adult shunt costs to nestling. Adults spend more time at sea to replenish adult body condition. This results in a decrease in the co-ordination of parental care.
Mechanism of parental provisioning	Observe Little Shearwater adult weights during nestling feeding	Preservation of adult body condition occurs, as weights are remained within an acceptable working range.
Mechanism of parental provisioning	Co-ordinated parental care in Little Shearwaters	Level of co-ordination appears to deteriorate during adverse years. Foraging is a flexible reactive behaviour.
Nestling growth	Examine weight gain over time.	Adults seem to meet needs of nestling in favourable years.
Nestling growth	Measure growth of nestlings	Growth rates differed between years
Nestling growth	Monitor feather growth	Feather growth is a continuous event, flight feathers grow later in development.
Little Shearwater foraging location	Forage near colony in cooler, inshore waters	Forage in deep water off the edge of the shelf in areas potentially affected by Leeuwin Current.
Little Shearwater dive depths	Small bird with narrow wings. Explore its dive potential.	Has potential to dive deep in keeping with leg morphology. Dive depth may be related to prey distribution rather than physical attributes?
Little Shearwater dive depths	Dive depth increases with time at sea Focus on different phases of parental provisioning	Dive depth recorded during long absence is greater than during short absence. Matches prey distribution?
Little Shearwater travel and weather	May utilise weather to travel to potentially distant locations	Arrival and departure of adults appeared to be linked to weather during incubation and nestling feeding
Little Shearwater	Investigate presence at colony at night	Present all night, <i>en masse</i> morning departure, therefore unlikely to forage at night. No squid observed in diet in this study, but others.
Wedge-tailed Shearwater	Investigate presence at colony at night.	Often depart after feeding nestling to forage at night, on squid? Not seen rafting near colony. Squid in diet.

**Table 9.5** – Continued. The objectives and outcomes of this study

Focus	Objectives	Outcomes
Wedge-tailed Shearwater travel and weather	Broad wings, able to survive low wind situations.	A decrease in provisioning was recorded during low wind conditions, associated with heat troughs.
Evaluation of stable isotope analysis	Seasonal changes in diet? Can direct comparison of meal sizes based on weight alone be conducted?	Meal sizes should not be compared by weight alone, as composition of diet varies with time and food delivered changes with age of nestling
Foraging at sea during egg membrane formation	Explore application of stable isotope analysis.	Wedge-tailed Shearwaters from the same colony appear to forage on similar resources during pre-laying exodus. Do decreased foraging constraints allow access of preferred food? Little Shearwaters appeared to target a more diverse range of foods. Not known if pre-laying exodus occurs, where foraging constraints are reduced. Wedge-tailed Shearwater colonies breeding on different islands often targeted different resources during egg formation.
Years of different quality	Observe provisioning patterns.	During favourable years adults appear to be able to meet nestling needs. This may define an optimal provisioning schedule. In adverse years more adults spend more time at sea replenishing adult body condition. A deviation from the optimal provisioning schedule occurs. Nestlings absorb the costs. Some pairs appear to be able to provide more food and a higher co-ordinated provisioning schedule than others. During adverse condition the number of pairs unable to do so appears to increase within the colony. This may provide an indication of pair quality, which affects proportion of cohort fed to obesity.
Nestling viability	Speculate on outcomes of the varied resource allocation pairs are able to invest in their offspring in years of different quality.	Deviations from the optimal provisioning schedule may reduce nestling viability. Reduced investment may reduce quality of feathers and post fledging buffer. This may affect fitness. The proportion of viable offspring within a colony may vary with quality of years. A difficult to measure implication of climate change?

In the winters of 2001 and 2002, during negative SOI conditions, the warm Leeuwin Current flowed weakly. Compared to years of positive SOI, offshore SSTs remained cooler, with little mixing and cross-shelf transport of nutrients to deeper water possible. The relatively high reproductive participation recorded in 2000, suggests that the Little Shearwaters capitalised on the mixing of warm tropical waters with cool waters, when the Leeuwin Current was strong. This is contrary to expectations created by their spatial distribution and physical attributes of the Little Shearwaters (Table 9.1), which suggest that the species is suited for cool waters.

## **9.2 Hatching and availability of resources**

Unlike many land birds, procellariiform eggs are able to withstand chilling, introducing a level of plasticity to the length of the incubation period (Warham 1990, Brooke 2004). However, at the Western Australian coast during the warm summer desiccation of eggs may be an issue, especially at lower latitudes despite insulation by the burrow. Nonetheless, this plasticity is thought to provide adults limited ability to time hatching in accord with oceanographic conditions (Warham 1990). In Little Shearwaters, the hatching period had a similar duration and central date in two successive years, despite differences in oceanographic conditions, suggesting that it may be entrained by a stable cue, such as photoperiod. Other studies have also found laying to be a relatively temporally predictable behaviour (Brooke 1978, Brooke 1990), which have traditionally allowed the harvest of muttonbirds (Brooke 2004). However, seabirds such as the Brown Noddies delayed the laying of eggs in a year of adverse conditions (Dunlop per comm. 2004), reminding that breeding is ultimately a resource dependent activity.

It is thought that the hatching patterns in a colony reflect the stability of conditions that permit breeding (Brooke 1990). This is highly influenced by latitude, with resources at higher latitudes collapsing in the absence of sunlight and giving rise to a need to migrate. On the central coast of Western Australia, 42 - 47 % of Little Shearwater nestlings hatched within three days of a central date in winter (Chapter 3). Thus, the Little Shearwater does not approach the extremely synchronous behaviour of species such as Short-tailed Shearwaters, (Serventy 1963, Klomp and Schultz 2000), whose foraging efforts target areas where seasonally available peaks of resources. Moreover, the absence of predictable peaks in resource availability may provide any incentive to shearwaters breeding in tropical locations to stagger breeding activities at a colony, as evident in the Christmas Island Shearwater and Audubon's Shearwater which hatch nestlings all year round (Harris 1969b). At the northern most part of its range, Little Shearwater reproduction appears to be sustained by a bimodal foraging strategy, which introduces the ability of adults to supplement local resources with distant resources, beyond a daily foraging range.

Over summer, 74% of Wedge-tailed Shearwater nestlings hatched within three days of a central date (Chapter 7). Similar results were obtained for the Wedge-tailed Shearwaters at Montague Island, on the eastern seaboard of Australia, where 64 % of eggs were laid within three days of a central date, compared to 84 % for Short-tailed Shearwaters at the same location (Schultz 1994). At the eastern sea board, the Short-tailed Shearwaters utilised a bimodal foraging strategy, where individuals foraged locally during short absences, but during longer absences sourced resources from Antarctic waters (Weimerskirch 1998, Klomp and Schultz 2000). Although, Short-tailed Shearwaters and Wedge-tailed Shearwaters breed simultaneously on Montague



Island, the breeding events of the Short-tailed Shearwater may be more synchronous, because its reproductive success depends upon highly seasonal resources at higher latitudes.

### **9.3 Foraging: the input system**

Seabirds breeding at a central location gather large amounts of food to feed to the dependent nestling at the breeding site. This suggests that a lot of seabird living is generally conducted at sea away from prying eyes and often little is known about the energy input system, which supports the dependent nestling. Both shearwater species studied delivered solid meals that were not infused with the stomach oil characteristic of Short-tailed Shearwaters (Warham 1990) which engages in a bimodal foraging strategy (Klomp and Schulz 2000). Little Shearwater regurgitates were difficult to obtain and consisted mainly of silver-grey fish slurry and copepod eyes, no stomach oils were detected despite the bimodal foraging strategy. Wedge-tailed Shearwater meals were similar in consistency, but squid pieces were frequently evident at Pelsaert Island, Rottneest Island and Lancelin Island. Both species fed semi-digested food to nestlings, which was of low fat content given its poor ability to stain clothes.

Presumably, the high frequencies at which birds returned to the colony did not necessitate the conversion of food into a lightweight, energy-rich concentrate of low nutritional value to enhance long distance flight, as do some shearwaters that forage more widely (Warham 1990).

Little Shearwaters carrying depth gauges reached a maximal depth of 33.7 m. In 2002, during incubation, they reached an average depth of 20.8 m during an average absence of 8.3 days. Whilst feeding nestlings, seven long absences averaged 8.9 days

during which an average depth of 28.1 m was reached; whilst provisioning a nestling daily, an average depth of 16 m was reached.

Observations at sea suggest that Little Shearwaters foraged west of the Abrolhos Islands, in deep waters beyond the edge of the continental shelf. When an adult returns daily to feed its nestling, Little Shearwaters clearly had a limited daily foraging range of approximately 70-170 km depending on flight speed, since they arrived early in the night and stayed at the breeding colony until dawn. At the Western Australian coast, Little Shearwaters were observed to engage in a bimodal co-ordinated foraging strategy, as also observed for the species in New Zealand (Booth et al 2000b). During longer absences Little Shearwaters have the potential to cover long distance away from the central breeding location. A preferred foraging range of 40-120 km was estimated for Wedge-tailed Shearwaters from Western Australia, with a maximal range of 234 km (Integrated Shearwater Monitoring Program 2000).

Given the time spent at the colony, Little Shearwaters spent less time at sea when attending to the nestling daily and thus had less opportunity to forage, during a 24 h period than Wedge-tailed Shearwaters, which arrived in the middle of the night and departed soon after feeding their nestlings. They were not observed to raft on the water near dusk or dawn. Similarly, short duration nestling attendance was documented at the North-West Shelf, in 1998 a less favourable year a mean duration of visitation by Wedge-tailed Shearwaters was 9.5 minutes was recorded, whilst in a more favourable year for seabird reproduction in 2000 the duration of visits increased to 11.6 minutes (Nicholson 2002). At the North-West Shelf, the duration of visits by

adult Wedge-tailed Shearwaters decreased with age of nestlings (Nicholson 2002). Overall, Wedge-tailed Shearwaters often had the opportunity to feed at night (Gould 1966), when they may hunt for the squid noted in their diet. However, such behaviours may change with location and time.

Little Shearwaters were not observed to scavenge behind boats and were not seen in foraging associations composed of different species near the islands. In contrast, Wedge-tailed Shearwaters did scavenge behind boats, foraged near the islands and were observed in feeding associations composed of pelagic fish and other seabirds in surrounding waters, as also observed in other studies (Jaquemet et al. 2004).

In the winters of 2001 and 2002, during negative SOI conditions the Leeuwin Current flowed weakly. Consequently, offshore SSTs remained cooler, with little mixing and cross-shelf transport of nutrients to deeper water possible, compared to years of positive SOI. The relatively high reproductive participation recorded in 2000, suggests that the Little Shearwaters capitalised on the mixing of warm tropical waters with cool waters, when the Leeuwin Current was strong. This is contrary to expectations created by their spatial distribution and physical attributes of the Little Shearwaters (Table 9.1), which suggest that the species is suited for cool waters. It however is in keeping with observations of the species at sea (Chapter 8), as they were also not observed to forage in the cool, inshore shelf waters. It is also consistent with observations by fishing industries that productivity along the Western Australian coast appears to decrease during years associated with negative SOI

Stable isotope analysis of egg membranes suggested that Wedge-tailed Shearwater females from the same colony foraged at a similar food chain, trophic level or focused on similar resources, if not foraging sites. During a pre-laying exodus females would have the ability to seek specific sites and forage on preferred prey in the absence of foraging constraints. The egg membranes produced by Little Shearwaters breeding on Beacon Island were not clumped, indicative of dietary differences within a colony. It is not known if a pre-laying exodus occurs in the Little Shearwater at this location, which would remove foraging constraints. Most Little Shearwater females appeared to forage at a lower trophic level than Wedge-tailed Shearwater females, similar in position to bait-fish such as Scaly Mackerel. However, some individuals showed the potential to access a higher trophic level. This may match the squid observed in the diet of Little Shearwaters, in other studies (Storr 1986). Foraging may be a flexible and potentially behaviour subject to availability of food, as indicated by stable isotope analysis in the Little Shearwater. Indeed the diet of Wedge-tailed Shearwaters appeared to shift seasonally during the development of the nestling, as shown by stable isotope analysis of feathers grown in different months. Seasonal changes in diet have been recorded in other studies (Warham 1990). A dietary study of both species could reveal interesting seasonal changes and shed light on the inter-annual changes in food availability and productivity along the Western Australian coast in relation to prevailing SOI.

#### **9.4 Evaluation and use of stable isotope analysis**

Stable isotope analysis promises to be a valuable tool to elucidate the behaviour of pelagic seabirds whilst absent from the colony, which are otherwise difficult, expensive or time consuming to observe or quantify. In this study stable isotope

analysis displayed differences in diets between different species engaged in similar activities (egg membrane formation), differences in diet between conspecifics breeding at different locations engaged in the same activity and seasonal changes in diet of birds breeding at the same location. It also served to investigate potential competition between seabirds and fishing industries (Bearhop et al 2001), as for the Little Shearwater during egg membrane formation. Along the Western Australian coast, diverse assemblages of seabirds which often breed at distant locations and other predators, such as sharks, have been observed to scavenge on bait discarded by the Western Rock Lobster Industry (pers. observ). This has implications on energy flow in ecosystems and the certification of ecologically sustainable fisheries, especially where imported bait is released into an ecosystem to attract catch (Dunlop pers com. 2001). Under the federal *Environmental Protection and Biodiversity Conservation Act 1999* state and federal fisheries should be managed to prevent overfishing and to minimise impacts upon the structure, productivity, function and biological diversity of the ecosystem.

Changes in diet were recorded within a species during the breeding season using stable isotope analysis, based upon understanding of time specific nature of plumage growth. This would have been extremely time consuming to demonstrate using dietary analysis. Consequently, an understanding of the time-specific nature of material deposition can be used to target resource allocation by the adult and provide a snap shot of adult foraging efforts. Materials can be collected with minimal time input, during a single or small number of visits to a colony. Materials are inert, robust and easy to store. Future research could focus on difference in diet in relation to variable oceanographic conditions within and between years and relate these to levels

of parental care. Better resolution and interpretation of data will be achieved once reference libraries have been established and the technique promises application in both scientific and applied research (Dunlop et al. unpublished).

## **9.5 Co-ordination of parental provisioning in a variable environment**

During both incubation and nestling feeding, Little Shearwaters alternated between periods of intensive care to support the offspring associated with overall weight loss, and longer absences from the colony, during which the weight loss was recovered. This suggests that adults present at the colony operate above an individual threshold weight and within an acceptable “working” weight range. The upper weight range may be defined by constraints associated with flight or temporal constraints associated with their partner’s depreciation in body condition who is attending to the progeny, which may lead to a decrease in parental care. This could endanger the current reproductive investment and ultimately adversely affect life-time reproductive success.

In 2002, incubation shifts averaged in duration of 7.5 days (range 5-11 days) for Little Shearwaters. It seemed as if the return of the relieving adult determined the length of the incubation shift, since change-overs were highly co-ordinated. On Beacon Island egg neglect may be low (5 % of change-overs) because of predation rates, as an unattended egg had a 24 % chance of being predated. Although, it is advantageous for members of a pair to maintain continuity of care, if one adult was away for too long, usually around nine days, the incubating adult departed. Presumably, these individuals terminated their incubation shifts when they reached an individual

threshold weight. In other species critical adult weights have determined the duration of the incubation shift rather than fixed temporal patterns (Chaurand and Weimerskirch 1994a).

All Little Shearwater hatchlings were brooded for at least the first day and most for the first three days. Little Shearwater nestlings appeared more able to miss a meal once a critical post-hatching weight had been reached, suggesting that supplementary feeding by adults during the first few days after hatching is important. Nestlings left alone the day after hatching may have been attended to by an adult near the end of the incubation shift, after a period of extensive fasting, and therefore unable to feed the nestling. Usually, an adult returned the following night, presumably to feed the nestling. This is indicative of the importance of supplementary feeding to supplement the egg yolk, to ensure the nestling exceeds a viable weight.

For Little Shearwaters, an average duration of incubation shift of 7.5 day was recorded towards the end of the incubation period associated with an average weight loss of 5.8 g/day (or 3 % of the average adult weight). Peaks of incubation change-overs occurred at intervals of about 3 to 4 days, indicative of some co-ordinating event such as weather. Similarly, during a time when the asynchronous colony moved from incubation to nestling feeding, Little Shearwaters appeared to use the predictable changes wind direction, associated with passing of weather systems, to assist their return to the colony. This rhythm of adult attendance may have arisen through asynchronous laying and been set by the relatively regular frequency of fronts passing across the Western Australian coast in early incubation. The pattern of change-overs

between adult attending may persist later in the nestling feeding period especially in species engaged in bimodal foraging (Brooke 2004).

During nestling feeding when adults co-ordinated a dual foraging strategy the partner attending to the nestling lost 5 g/day (or 3 % of the average adult weight). Whereas adults returned heavier from the long absences, which indicated that these served to replenish adult body condition. Similar increases in body condition have been observed during long absences during nestling feeding in the Blue Petrel *Halobaena caerulea*: (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 2003), Wandering Albatross *Diomedea exulans* (Weimerskirch 1995), Sooty Shearwater *Puffinus griseus* (Weimerskirch et al. 1994, Weimerskirch 1998) and Short-tailed Shearwater (Klomp and Schultz 2000). The duration of long absences appeared to increase in a less favourable year, when adults presumably took longer to recover body condition, resulting in a disruption in provisioning. The reactive nature of foraging in response to changes in oceanographic conditions requires further research attention.

Both species were able to meet nestling needs in a favourable year, when mass gain of nestlings and the amount of food delivered throughout growth followed a similar pattern. During a less favourable year, meal sizes delivered by the Little Shearwaters were more erratic and smaller. Nonetheless, adults still increased provisioning with the age of their nestling, albeit at a lower rate. Subsequently, the weight gain in nestlings occurred at a lower rate in a less favourable year, when nestling weights also reached a lower asymptote. This reduced level of input resulted in lower growth rates, despite nestlings reaching larger asymptotes for some skeletal measurements, except tarsus lengths, which was similar between the years. Overall, adults shunted



costs to the nestlings during a less favourable year by reducing food delivery. In turn, offspring may alter resource allocation to foremost satisfy essential attributes, possibly to meet the strong selective forces of the ocean.

During less favourable years, only higher quality pairs can source sufficient energy to participate in reproduction, and only a subsection of this breeding colony can maintain a high level of parental care, whilst a large proportion of the colony may shunt cost to the offspring. These more subtle changes in along a continuum in the level of parental care allocated by adults will have differential effects on nestling viability and may influence the life-time reproductive success of individuals. Consequently, climatic change has the potential to affect the proportion of nestling produced in a cohort, which fledge after optimal provisioning and with maximal survival chances.

If resources levels could maintain an acceptable adult body condition, then adults are able to meet nestling needs (Tveraa et al. 1998, Varpe et al. 2004), whilst a deviation from an optimal provisioning schedule appeared to occur during less favourable conditions. Given that provisioning is dependent on the state of the adult and therefore clearly a highly flexible reactive trait, characteristic values that describe provisioning by a species (i.e. meal sizes) which can easily be compared between colonies and years, may be difficult to define. Furthermore, the needs of nestlings change during ontogeny, making it possible to at the best define an optimal meal size (of unknown calorific and nutritional value) for a given developmental age.

Little Shearwaters, breeding in winter, were able to deliver food at a more regular rate than Wedge-tailed Shearwaters whose nestlings, even during a favourable year,

experienced periods of reduced provisioning that resulted in nestling weight loss. In Wedge-tailed Shearwaters, in all years and at different latitudes along the Western Australian coast, periods of weight loss by nestlings coincided with periods of low winds, associated with dissipating tropical lows generated by areas of elevated SSTs travelling southwards. Such weather patterns are a predictable seasonal occurrence along the Western Australian coast. However, the frequency of such weather systems increases during certain climatic conditions, particularly during El Niña conditions and during transition years from one extreme to another. When warm SST prevail to the north of Australia, tropical lows are more likely to form and persist, which may turn into tropical cyclones or heat throughs depending on intensity, both associated with adverse proximal conditions.

In the 1999/2000 breeding season, a transition year suitable for Wedge-tailed Shearwater reproduction, supplementarily fed Wedge-tailed Shearwater nestlings were fed less by their parents during periods of adverse wind conditions, than nestlings that were not supplementarily fed. In such species, whose adults frequently visit the nest, parents may react to the condition of the nestling when orchestrating a delivery system, and thereby protect their own body condition during adverse travelling conditions. Once weather conditions had improved, parents of supplementarily fed young who had reduced provisioning during less favourable travel conditions were able to feed their nestlings at a higher rate, than those whose nestling had not been supplementarily fed. This suggests that that the latter were unable to capitalise upon good conditions in terms of food delivery to the nestling.

Although both species frequently and regularly fed their offspring, nestlings still peaked well above adult weight (Table 9.4). Daily feedback on nestling condition means that chronic overfeeding in the absence of feedback (Ricklefs and Shew 1994) is not a plausible reason. Since food delivery occurred near daily it suggests that obesity is not necessarily a buffer against stochastic provisioning, a conclusion also advanced for Little Shearwaters in New Zealand (Booth et al. 2000). However, the Western Australian coast lacks temporally and spatially stable zones of oceanographic productivity, so that adults may overfeed to offset expected unpredictability in oceanographic conditions. Obesity may be utilised to immediately buffer dependent nestlings against a disruption in food delivery, caused by unpredictable events, such as reduction in resource availability and adverse weather conditions which do not facilitate foraging or travel. However, obesity may be used by adults to obtain direct benefits for their progeny in terms of post-fledging fitness for the independent fledgling attempting to survive at sea. The latter seem plausible, given that weight loss prior to fledging involves a reduction in water content rather than shedding of lipids.

Nestlings of both shearwaters studied were not deserted during the weight recession phase, although the rate of provisioning decreased. This is in keeping with the absence of seasonal temporal constraints at these lower latitudes. However, in both species, differences in pre-fledging provisioning were noted between pairs, with some nestlings unfed for an extended period of time. In Wedge-tailed Shearwaters, the metabolic rate of nestlings did not change with their feeding history, but water loss was greatest in birds closer to fledging. This suggests that pre-fledging weight loss is associated with water loss. This is supported by other studies of procellariiform

nestling composition, in which the water composition of nestlings decreased before fledging, whilst lipid composition did not (Phillips and Hamer 1999, Powell 2004). Nestlings able to fledge with good fat stores, or at least a post-fledging buffer, may have had a greater chance of survival during the transition from dependent nestling to autonomous young adult. It is expected that high risk periods for nestling mortality, when nestlings are young, are matched with favourable conditions that allow adults to provide appropriate levels of care to minimise risks to their investment.

Little Shearwater adults appeared to adjusted parental provisioning in accord with prevailing conditions, foremost to protect themselves and possibly the condition of their partner, since breeding success increases in shearwaters with duration of pair bond (Brooke 2004). During all stages of provisioning, adults lost weight and each phase, effectively, was a filter to reproductive success. During incubation, birds fasted, but the risks of predation encouraged co-ordinated change-overs, despite eggs being able to withstand periods of chilling. During nestling feeding, especially once nestlings were larger and less vulnerable, provisioning schedules could be adjusted. It suggests that most studies on provisioning have focused on the most forgiving and malleable stage, one easily influenced by environmental conditions. In most studies of similar species, nestling mortality is low, and most nestlings fledge. However, inter-annual differences in survival after fledging, which are very difficult to measure, may result from differences in the deviations from an optimal parental provisioning schedule.

## **9.6 A tentative model of adult state-dependent co-ordination of provisioning**

The allocation of parental provisioning appeared to be foremost dependent upon the ability of the adults to maintain their body condition. Secondly, if adults are able to maintain or replenish their own body condition parental care was tailored to meet the needs of the nestling. An optimal provisioning pattern of parental care emerged under favourable conditions when adults are able to meet the needs of the nestling, however deviations from this optimal pattern were observed as oceanographic conditions were less favourable, possibly because adults spent more time at sea replenishing body conditions.

If an adult was unable to replenish its body condition in a time period matching the acceptable weight losses range experienced by the partner engaged in intensive parental care, the co-ordination of parental care decreased and a deviation from an optimal provisioning pattern occurred. Consequently, the ability to replenish adult body condition in a timely manner appears to be a major factor in determining the pattern and co-ordination of parental care observed. Ability of adults to replenish body condition is dependent not only upon resource availability but also proximal weather conditions that affect foraging or travel. When possible, adult appeared to make use of favourable weather conditions for travel, possibly to minimise energy expenditures. However, adults have been observed to fly through adverse systems (Murray et al 2002), potentially reflecting inexperience or certainty of the ability to replenish such expenditures at a later date. Deviations from the optimal pattern of parental care fail to meet the nestling needs and are indicative of the pairs' inability to

operate above a threshold adult body condition with prevailing environmental conditions. Consequently, as conditions deteriorate, a smaller proportion of pairs are able to maintain a uniform, co-ordinated system of food delivery and a larger proportion of nestling of a cohort are fed less than optimally.

Attempts to weigh adults, should provide little indication of favourable or less favourable years, as only adults above a threshold body condition are encountered at the breeding colony. Therefore, adults encountered at the colony operate in a working weight range as during most phases of provisioning, adults are expected to absorb regular declines in adult body weight associated with reproduction at a central location, down to an individual threshold weight. It is the ability to replenish acceptable and to prepare for repeated weight losses and thereby maintain an acceptable working weight range, which determine the level of care provided to a nestling at a central location. In a favourable year, adult body condition can easily be replenished, within a time frame compatible with the need of the adult currently attending to the nestling. Consequently, near continuous parental care results. A highly co-ordinated parental provisioning is only expected to emerge in a favourable year. Here adults have the capacity to meet nestling needs closely, as evident in 2000, when food delivery consumption by nestlings mirrored the pattern of weight gain characteristic of shearwater nestlings. The ability to adjust provisioning in accordance with nestling needs has been observed in many other studies (Bolton 1995, 1995b, Hamer and Thompson 1997, Bradley et al. 2000).

During a less favourable year, adults may struggle to gather sufficient energy to cover the elevated needs and maintain adult weights above a threshold weight. As a result,

Little Shearwater adults appeared unable to meet the needs of the nestling in a less favourable year. This suggests that adults will shunt costs to the offspring (Muck and Grubb 1995) whenever conditions make it difficult to meet their own needs. Overall, adults are able to respond to nestling needs, providing their body condition allows, based on the maintenance of a threshold adult body condition (Tveraa et al. 1998, Granadeiro, 1998). Such state-dependency has also emerged in studies focusing on the adult's ability to co-ordinate guarding of hatchlings (Varpe et al. 2004). This suggests, below a threshold further provisioning is withheld, whilst above a threshold adults chose to respond to the needs of the offspring, limited by the ability to replenish or maintain their own body condition. A two-tier system appears to exist that influence the action of adults and the level of parental care provided.

At the Houtman Abrolhos Islands, food delivery was adjusted to suit nestling needs in good years and adults appeared to co-ordinate provisioning, albeit within the limitations needed to maintain adult body condition. An underlying threshold adult body condition has been proposed in many studies (Muck and Grubb 1995, Granadeiro 1998, Tveraa et al. 1998, Takahashi et al. 1999b). In contrast, in the northern hemisphere, Little Shearwater meal size and feeding frequency appeared not to be adjusted to the nutritional status of the nestling. Rather, provisioning patterns, determined over a relatively short period of time, suggested that adults acted in accordance with intrinsic rhythms, independent of the nestling (Hamer 1994). This is in keeping with several manipulative studies, in which increased demand at the nest was not met (Ricklefs 1987, 1992, Hamer and Hill 1993). Unfortunately, most studies of Procellariiform provisioning have not been anchored to an index of oceanographic productivity to provide the context in which to interpret the adult

response, as for example an “ inability to respond” may reflect “insufficient resource availability or proximal weather conditions” that allow timely replenishment or maintenance of adult body condition. Under favourable conditions, when adults easily maintain or replenish adult body condition, adults will also be able to react to increased demands at the nest however in less favourable year the same individuals will years they will not do so. This may have generated the variable and often contradictory outcomes generated by experimental studies of parental provisioning, which were not viewed in context of prevailing climatic conditions. Seabirds operating on an adult state-dependent system of parental provisioning will react in accord with the limitations imposed by the environment.

Provisioning appears to be a flexible behaviour, which allows long-lived, iteroparous species to react to proximal conditions, and ultimately, to breed in both stable and also less stable environments. However, to protect the annual reproductive investment, ideally energy frugality should be shunted away from sensitive periods of nestling development, such as the guard period after hatching, when nestlings are vulnerable. However, foremost provisioning is dependant upon the state of the adult in light of resource availability and energy budgeting, as travel appears to be assisted by favourable weather systems where possible. The Western Australian coast can be viewed as a highly unpredictable oceanographic region, where state-dependent reactions are more likely to surface. The Little Shearwater engages in bimodal foraging where adult state dependent behaviour is likely to emerge. In other bimodal foraging species adults have been observed to replenish body condition during long absences from the colony (Chaurand and Weimerskirch 1994b, Weimerskirch et al. 1994, Weimerskirch 1995, Weimerskirch 1998, Klomp and Schulz 2000).



The deviation from an optimal provisioning schedule may influence nestling growth however strong stabilising selective forces govern survival at sea (Bull 2004) and should limit the magnitude of change in skeletal morphometrics. Consequently, nestlings are expected to allocate resources to fixed structural components and shunt energy deficiencies towards changing attributes, such as decreased feather quality and lower fat reserves. Both short cuts in material allocation by the nestling in response to decreased adult investment may decrease potential survival chances of the nestling after fledging. It however, gives the individual the opportunity to ameliorate a less than optimal start to life. Given that the availability of ocean resource is often spatially and temporally unpredictable, chances are reasonable that good conditions may return or can be found further away from the breeding colony.

#### 9.6.1 Future research

Future research directions are listed in Table 9.6 and aim to further explore the adult-state depended system of co-ordination of continuous parental care (section 9.5).

Future research should focus on the ability of the members of pair to maintain their collective body condition in variable oceanographic conditions and how costs are passed on to the offspring. As it becomes more difficult to maintain parental body conditions, adults are expected to remain at sea for longer which decreases the ability of the pair to provide co-ordinated continuous parental care, resulting in a deviation from an optimal provisioning schedule. Whilst during favourable periods, when it is relatively easy to maintain adult body condition it is expected that adults will be able to deliver optimal parental care and even respond to increased demands at the nest

site. This process may also be observed within breeding population in a given year, as some pairs appear to be better parents than others. Future research should also investigate the implications of the model on the nestling, as this may give an indication of the likely effects of climate change.

**Table 9.6** Future research directions

Future research directions	Potential objectives
Studies of parental provisioning viewed in context of oceanographic conditions	Anchor adult behaviour to an index of oceanographic conditions to gain a better understanding of the allocation of parental care. Attempt to define optimal parental provisioning under optimal conditions where nestling needs should be met. Document deviations from the optimal pattern, with increased costs to adults in a system that cannot cover increased costs (i.e. adverse year, inexperienced birds).
Automated means to monitor arrival and adult attendance at nests in years of different conditions	During adverse conditions adults should spend more time at sea to replenishing body condition - this can occur during incubation and nestling feeding
Experimental studies that increase adult costs foraging at sea	Higher costs should increase the time taken by adults to return to the colony. Possibly best suited for bimodal foragers.
Focus on adult weights and how weight loss affects co-ordination of parental care	A relatively constant working range of adult weights should be observed at the colony. Whilst during less favourable conditions a decrease in the co-ordination of parental care and input to the nesting should emerge. Adults are expected to stay at sea to replenish body condition.
Identification of how the costs shunted by the adult to the offspring are assimilated by the offspring	Does the level of obesity reached within a colony change between years? Is feather quality lower, with focus on fault lines and structural integrity? Do such factors effect fledgling survival, recruitment or fitness?
Stable isotope analysis	Establish a prey library using stable isotope analysis Gain a better understanding of resource targeted by a large suite of oceanic predators to view ecosystem dynamics Compare time-specific materials between years of variable oceanographic conditions and document levels of parental provisioning. During adverse years a larger range of prey items are expected in the diet, potentially resulting in a decrease in trophic level, as foraging constraints result in a decrease in choice.

In this study, during a less favourable year (2002) lower rates of provisioning, increased irregularity of provisioning, decreases in skeletal growth rate and lower weight increases were recorded for Little Shearwaters compared to a favourable year (2000) (Chapters 4 and 5). At the eastern seaboard in the 2002/2003 breeding season when El Niño conditions continued to intensify, decreased meal size, provisioning rates and weight gains were recorded in Wedge-tailed Shearwaters nestlings during periods of elevated SST, suggesting that parents passed on costs to the nestling (Peck et al. 2004). In this study, Wedge-tailed Shearwaters decreased provisioning rates during periods dominated by tropical lows, when low wind conditions were experienced (Chapter 6). Tropical lows are small scale weather systems that are generated and sustained by the movement of warm tropical water to the south (Chapter 1). Both studies suggest that under less favourable conditions, here associated with elevated SSTs, either within a year or between years, adults passed on costs to the nestling. Unfortunately, the dependent nestling only has one chance for survival and needs to accept the level of parental care allocated by the adults under prevailing conditions. Prevailing conditions encompass any factor that may influence the ability of adults to maintain their body condition above a certain threshold whilst working to meet reproductive demands, and may include resource availability, location of resources, ease of travel to and from foraging sites. Therefore, the ability of adults to maintain an appropriate body condition is not only influenced by large scale changes in SST that affect oceanographic resource levels, but also by short term weather conditions formed above the earth's surface of varied thermal properties (including SST) which affect locomotion.

Optimal pattern of parental provisioning may be adopted when favourable conditions prevail and such patterns would meet the needs of the nestling optimally. During less favourable conditions, the nestlings need to assimilate deviations from an optimal provisioning schedule in a way that minimises risks to the survival of the nestling. The nestling may be limited in its ability to shunt costs to skeletal dimensions, as these should be relatively fixed to suit a niche, given the strong selective force exerted upon the functional adult by the oceanographic environment (Richdale 1957, Lack 1968, Ashmole 1971). Consequently, costs are expected to be shunted to dynamic short-term features, such as fat stores and quality of feathers, which can be addressed by the nestling once independent and energy input is no longer constraint around a central location. Although, nestlings may fledge, developmental deficiencies may adversely affect post fledging survival as the fledging needs to overcome a less than optimal start to life. This can be fatal for a novice hunter.

The decreased ability of the adult to invest in the nestling has the potential to increase the costs which have to be covered by the nestling. After fledging the progeny has to learn how to feed independently and a lipid buffer may be advantageous. Whilst, a fledgling with a less than optimal plumage experiences higher flight costs and is faced with a major resource investment earlier in independence than fledglings which have been endowed with plumage of higher structural integrity. Consequently, the variable allocation of resources by adults may determine the level of post-fledging buffer provided to the offspring. In the quest for survival, the offspring may encounter conditions sufficient to ameliorate the short comings generated by the adult state-dependent co-ordination of parental care provided by adult K-strategists attempting to survive in a relatively unstable, unpredictable environment. After fledging, the

offspring and the breeding population are no longer tied to a central location, which greatly enhances the potential to seek areas of high productivity. Climate change has the potential to changes in oceanographic conditions (especially SSTs) and resources levels. Resultant changes in parental investment in the offspring quality or viability has implications on population dynamics, especially in terms of recruitment, in long-lived, pelagic seabirds.

## **9.7 Constraints of the input system**

The ability of adult shearwaters to source resources at sea is dependent on their availability and accessibility, within an acceptable distance from the central location to produce a surplus energy budget. Time and energy budgets may be affected by predictable seasonal factors but also less predictable changes within and between years, including climate change. Behavioural flexibility allows individuals to react to unpredictable influences.

Wedge-tailed Shearwaters colonies breeding at the Western Australian coast appeared to forage in areas influenced by the flow rate of the Leeuwin Current, which presumably explained why breeding participation and success appears to closely fluctuate with the SOI. In summer, the Leeuwin Current flows more slowly and the strong southerly winds that prevail often result in net northward movement of water. Nonetheless, offshore sea surface temperatures are still affected by the preceding flow rate of the Leeuwin Current. Wedge-tailed Shearwater nestlings hatched, when the southerly winds are expected to disappear, coinciding with the predictable dissipation of tropical lows in late January to May. There may thus be selective pressure upon Wedge-tailed Shearwaters along the Western Australian coast to hatch nestlings so

that they are sufficiently large and robust to withstand periods of poor provisioning during low wind conditions. This may influence hatching dates.

SOI conditions influence annual weather, and thereby affect the energetics involved in seabird travel, as well as the likelihood that catastrophes might terminate breeding efforts. In transition years, when the El Niño breaks down, the frequency of tropical cyclones appears to increase along the Western Australian coast, especially in March, when the warm Leeuwin Current begins to flow and the warm water has the potential to feed the cyclones (Meteorology 1998, Colls and Whitaker 2001). At the North-West Shelf, Wedge-tailed Shearwater reproduction may be terminated by catastrophes, such as tropical cyclones. This was the case in 1998/1999, after a strong El Niño year, when Tropical Cyclone Vance appeared late in March 1999 (Integrated Shearwater Monitoring Program 2001). Similarly, in 2003/2004, when a phase of El Niño conditions subsided, the North-West Shelf was battered by strong winds and heavy rains associated with Tropical Cyclone Monte, in late March 2004 (Integrated Shearwater Monitoring Program 2006). At the central Western Australian coast, cyclones are rare, but the heat troughs associated with dissipating tropical cyclones, expected in late January to May, result in prolonged periods of low winds that are likely to impede Wedge-tailed Shearwater travel and result in periodic reductions in nestling feeding (Chapters 6 and 7) that adversely affect nestling weight gain.

Little Shearwaters breed in winter at the Houtman Abrolhos Islands, at the northern most limit of their range on this coast using a bimodal foraging strategy. During a favourable year an optimal provisioning schedule is highly co-ordinated, whilst in less favourable years, deviations arise. Most likely the delays in the return from foraging

sites may be linked to the inability of adults to replenish body condition and travel also appeared to be weather assisted. Consequently, proximal conditions may influence colony attendance. Fronts might assist travel during pre-laying and incubation in winter, when low wind speeds are experienced along the central coast of Western Australia. Weather assisted travel appears to have been observed in Short-tailed Shearwaters utilising the northern edge of the roaring forties to travel eastwards (Klomp and Schulz 2000). However, intent to reach destination remain, rather than being a passive response to weather systems, as individuals would even fly through complex weather patterns (Murray et al 2002). Battling with weather systems is expected to be more energy expensive than hitching a ride with a favourable system. The extent to which large fronts reach up the Western Australian coast may even delimit the northernmost breeding distribution of Little Shearwaters, especially during incubation when otherwise relatively low winter wind conditions prevail. The frequency and intensity of fronts and their ability to influence northern region appears to vary with global climatic conditions. Consequently, climate change may influence adult attendance patterns during the relatively sensitive incubation period and create a bottle neck period. Hatching of nestlings and increased energy delivery to the breeding location to facilitate nestling growth may be timed to utilise the more reliable travel conditions generated by seasonality through the onset of southerly winds. Strong winds are associated with the southern movement of the belt of high pressure systems (Chapter 1).

Little Shearwater nestlings hatched in September when a transition from the winter pattern- where fronts reach northwards, to the summer pattern- where the belt of high pressure cells move southwards (Chapter 1). From October to January, strong

southerly winds associated with the high pressure cells are a predictable feature of the oceanographic environment and may assist seabird travel; this is when most seabirds reproduce on the central Western Australian coast. However, the onset and strength of southerly winds appears to be influenced by climatic events. Climatic averages should be generated for periods of positive and negative SOI. For example, during El Niño years or prolonged negative SOI, extremely strong southerly winds appeared to prevail, which began earlier in spring and persist for longer in autumn. Whilst during periods of positive SOI heat troughs and low wind situations appeared to be more prevalent in late summer and autumn. Consequently, on average summers during El Niño years may be associated with greater wind strengths than La Niña years along the Western Australian coast, whilst the frequency of cold fronts reaching the mid-west coast may be lower in El Niño years than La Niña years. This suggests that climate change has the potential to influence locomotion of colonial breeding seabirds, which appear to overcome competition by covering large distance during foraging from a central breeding location. Climate change also appears to affect oceanic resource levels with a potential crash in productivity associated with prolonged negative SOI or El Niño years along the Western Australian coast.

The strategy employed by adults to source food from spatially separated foraging sites may vary with location, in accord with resource availability and costs. This may explain why Wedge-tailed Shearwaters at different locations have been recorded using both a unimodal (Baduini 2002) and a bimodal (Congdon 2003) foraging strategy. It also demonstrates an inherent flexibility in such behavioural traits within a species, although the extent of flexibility remains to be determined. It is not known how far foraging can be adjusted between years, to cope with variability in resource



distributions, such as that recorded at the Western Australian coast. This has clear implications for seabird reproduction in response to climate change.

## **9.8 Climate change and reproductive output**

Climatic change has the potential to influence reproductive participation and breeding success (Warham 1990, Smithers et al. 2003, Brooke 2004), through an alteration of foraging conditions or catastrophes. Foraging conditions include both resource availability and proximal weather conditions that may affect travel and energy expenditures. Reproductive effort was adjusted in a more subtle manner, than more easily measured changes in breeding participation and breeding success. At the Western Australian coast, seabird has been documented to change with inter-annual variations in SOI values (Wooller et al. 1991, Integrated Shearwater Monitoring Program 2000, 2001, Surman 2001, Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, Surman et al. 2002, Integrated Shearwater Monitoring Program 2003, 2006). Here, inter-annual variations in climate also affected parental provisioning and nestling growth rates in Little Shearwater. At the east coast, Wedge-tailed Shearwaters also reduced parental provisioning, and consequently weight gain decreased in nestlings during a years associated with increased breeding failure (Smithers et al. 2003). Such deviations from optimal parental provisioning suggest that adults are limited in their ability to compensate for changes in foraging conditions. The tentative model of where parental provisioning is dependent upon the state of the adult may provide a mechanism to explain the subtle adjustments in parental investment observed. These more cryptic adjustments, made during provisioning, suggest that climate change puts further stress on the adults, which are

passed on to the nestling. Most importantly, sub-optimal levels of provisioning may reduce post-fledging survival during adverse years.

A crash in productivity along the Western Australian coast in response to cooler offshore waters as a result of reduced Leeuwin Current flow has been proposed, with tropical seabirds breeding performance reduced during periods of negative SOI (Dunlop et al. 2002). In the summer of 2002/2003, the reproduction of Common Noddies was depressed at the Abrolhos Islands (Dr Chris Surman 2004, pers. comm.) and Lancelin Island (Dr Nic Dunlop 2004, pers. comm.). In the same period, other predators were also affected, as suggested by the low returns for effort experienced by the tuna industry during El Niño years (Craig Culliver 2004, pers. com.). Similarly, the settlement of Western Rock Lobster puerulus is low during El Niño events (Pearce and Phillips 1988, Kailola et al. 1993). For Western Rock Lobsters, an overall crash in offshore food webs, which failed to sustain the pelagic form, rather than adverse settlement conditions, was thought to be the cause (Dr Nic Dunlop 2003 pers. comm.). This has the potential to influence the reproductive participation of seabirds at distant breeding sites, given the diversity of species visiting the waters off the Western Australian coast during their non-breeding season.

Global climate change poses a real threat to seabird reproduction. Wedge-tailed Shearwater monitoring on Lancelin Island and Rottnest Island revealed that in 2000/2001, as well as in 2001/2002, Wedge-tailed Shearwater breeding participation rates were high, but that they decreased in 2002/2003 when El Niño conditions became established (Table 9.3). Similarly, long-term monitoring at the North-West Shelf revealed an even stronger trend and highlighted the susceptibility of Wedge-

tailed Shearwater reproduction to ENSO events (Dunlop et al. 2002, Integrated Shearwater Monitoring Program 2002, 2006). A similar decrease in reproduction and provisioning, detected in 2002 at the Great Barrier Reef during El Niño conditions, only at the east coast it was linked to an increase in sea surface temperatures (Peck and Congdon 2003, 2004; Smithers et al. 2003, Peck et al. 2004).

The sea surface temperatures along the Western Australian coast vary, with flow rates of the Leeuwin Current. During years of reduced current flow Wedge-tailed Shearwaters low reproductive participation was recorded in the south (Lancelin Island), whilst the warm water banked up around the North-West Shelf appeared to support Wedge-tailed Shearwater reproduction in 2006 in the north. However, the warm water also facilitated the formation and persistence of tropical cyclones with had random impacts in terms of nestling mortality (personal observ.). Whilst in other years, when colonies to the north displayed lower breeding participation than colonies in the south, indicative of low resource levels (Integrated Shearwater Monitoring Program 2003). This variable effect of sea surface temperatures, oceanographic productivity and random catastrophes may explain the marked increase in the number of breeding Wedge-tailed Shearwaters documented at Rottnest Island over the last few decades (Bancroft et al. 2004). The Western Rock Lobster fishery may provides food to supplement the feeding of nestlings (Dunlop and Asmussen unpublished), but should not effect breeding participation, as at the start of the season in November the vessels are working inshore.

Seabird species are mobile and have the potential to expand their range to make use of changing climatic conditions, as evident on the Western Australian coast by the range

expansion documented for the Red-tailed Tropicbird *Phaethon rubicauda*, Bridled Tern (Serventy et al. 1971), Roseate Tern (Dunlop 1979), Common Noddy (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001) and Sooty Tern (Dunlop and Mitchell 2001). The southwards extension of the Common Noddy and the successive establishment of a large breeding colony has been comprehensively documented and appears to be largely based on recruitment of adults from elsewhere (Dunlop and Goldberg 1999, Dunlop and Mitchell 2001). Such flexibility may allow seabirds to colonise new habitat if breeding sites are lost to sea level increases and local reduction in food availability.

Along the Western Australian coast, breeding performance of some seabirds may provide good indicators of oceanographic conditions which also affect local fisheries (Nic Dunlop 2000, pers comm.). This is especially true for species that forage within the area influence by the Leeuwin Current, such as the Wedge-tailed Shearwater. Conversely, species that source distant resources may not reflect resource levels in nearby waters. Thus, an inability to match Short-tailed Shearwater reproduction with fluctuations in ENSO events (Ron Wooller 2004, pers comm.), may relate to the partial reliance of this species on subantarctic resources at high latitudes, that only become seasonally available at a predictable time of year. Short-tailed Shearwaters breeding around south-eastern Australia use a bimodal forage strategy to forage in Antarctic waters (Klomp and Schultz 2000). However, foraging is flexible within a species as demonstrated by the Wedge-tailed Shearwater that may use a unimodal (Baduini et al 2002) or bimodal foraging strategy (Congdon et al 2003) in response to resource availability at a given location. This suggests that any indicator species should be chosen on the basis of the local foraging strategy and potential foraging

range, as to ensure that the area monitored is of key importance to the indicator. Existing seabird studies at the Western Australian coast have appeared to have targeted species that forage on, and at the edge of, the continental shelf and this may be why they so accurately track the influence of SOI events upon productivity off this coast. Long-term studies of predators dependent on local resources therefore have the potential to aid in the management of local fisheries along the Western Australian coast, using suitable seabird species as robust, reliable and cost-effective indicators. Further research focused on seabirds (Table 9.6) may help to understand potential impacts of climate change on shearwater breeding populations.

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