

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,
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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.

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Indre Kirsten Asmussen

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I wish to thank everyone, who helped to makes this project a reality and shared life.

Abrolhos Islands and Geraldton

The study of Little Shearwater on Beacon Island would not have been possible without Ray and Faye Howarth and Bob Spence. Ray and Bob provided lifts to the Islands on the “Island Leader II” and were the only constants besides the birds and howling southerlies. Mainland support was provided by my family and friends in Geraldton. I was introduced to the Islands by Dr Chris Surman and I wish you, your wife Dr Lisa Nicholson and family happiness in the future.

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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. Fortunately, 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

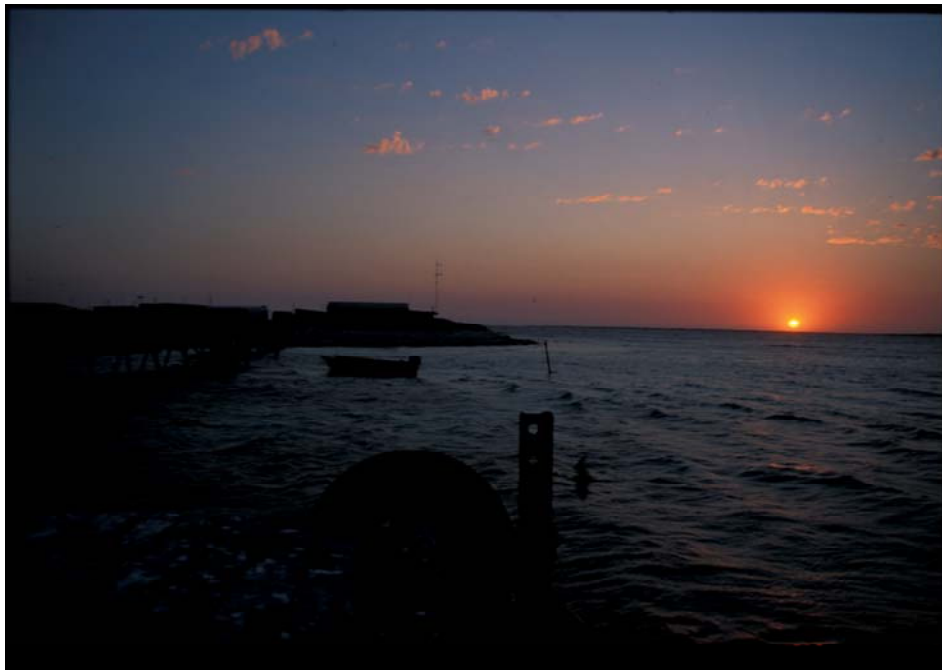


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