Feeding and Breeding Ecology of Little Penguins (*Eudyptula minor*) in the Eastern Great Australian Bight

Submitted by

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A thesis submitted in total fulfilments of the requirements for the degree of
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Thesis declaration

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This thesis is presented as a series of papers that will be submitted following examination. Although I did the significant aspects of data collection, analysis and interpretation of the results I offered co-authorship on papers to B. Page, S.D. Goldsworthy, D.C. Paton, N. Bool and T.M. Ward because they assisted in the pursuit of the research or preparation of the thesis: S.D. Goldsworthy, D.C. Paton and T.M. Ward supervised this project and received grants that funded part of this research.

All research procedures reported in the thesis were approved by the Animal Ethics Committees of the University of Adelaide, Primary Industries and Resources South Australia and the South Australian Department for Environment and Natural Resources (DENR). Permits were granted by DENR.

Annelise S. Wiebkin

…………………………….………………. June 2012

“Who would believe in penguins

unless he had seen them?”

Conor O Brien, *Across Three Oceans*

Abstract

This thesis investigated aspects of foraging and reproductive ecology of little penguins *Eudyptula minor* in the eastern Great Australian Bight. Little penguins are permanent residents in this region and the link between their ecology and their local food source is poorly understood in the Great Australian Bight. Most little penguin colonies in South Australia are small in population (< 4000 breeding individuals) and they are almost all found on islands. Despite similarities in breeding seasons and diet among colonies, the foraging ecology of penguins from offshore colonies differed from inshore colonies in the same region. Natural variation in diet and foraging behaviour at eight colonies was attributed to differences in food availability. Inter-colony differences in foraging behaviour and effort, which were consistent between years, were related to differences in penguin morphology, growth and body size. Breeding penguins from the offshore colony travelled up to 3 times further from shore (39 vs. 13-21 km) and for greater durations (3 vs. 1 days), and spent more time diving (56 vs. 37 % of foraging time). Results suggest that food availability is depleted, or not profitable in near colony waters, possibly as a consequence of increased or prolonged predation by the large penguin population. This study also indicated that increased foraging effort at the colony level was reflected in the growth parameters of offspring, because offshore colonies had smaller offspring and adults, and delayed development of sexual size differentiation in bill morphology. Increases in foraging distance and duration were also linked to poorer breeding success.

Little penguins at different colonies exhibited low variation in their diet because juvenile Australian anchovies *Engraulis australis* were mainly targeted as a food source. Dive behaviour was similar among colonies, despite differences in the depths around colonies. The regional availability and abundance of anchovies may be responsible for the unusual pattern of winter breeding that is apparent in South Australia. Little penguin diet, breeding and foraging parameters may provide quantitative indicators of the health of local anchovy stocks, especially if an anchovy fishery develops in South Australia. Baseline information on these penguin parameters parameters may also inform management decisions aimed at conserving penguin populations across the region.

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Table of Contents

List of Figures

Page

Chapter 1: General Introduction.

Chapter 2: Determining the sex of little penguins from South Australia using discriminant functions based on bill morphology.

Chapter 3: Do inter-colony differences in the morphology of little penguins result from differences in food availability?

Chapter 4: The diets of little penguins *Eudyptula minor* and their reliance on Australian anchovy *Engraulis australis* in South Australia.

Chapter 5: Does the diving behaviour of little penguins differ at sites where their primary prey can access different depths?

Chapter 6: Why are some little penguins so little: an effect of Ashmole's halo on foraging behaviour?

List of Tables

Page

Chapter 2: Determining the sex of little penguins from South Australia using discriminant functions based on bill morphology.

Chapter 3: Do inter-colony differences in the morphology of little penguins result from differences in food availability?

Chapter 4: The diets of little penguins *Eudyptula minor* and their reliance on Australian anchovy *Engraulis australis* in South Australia.

Chapter 5: Does the diving behaviour of little penguins differ at sites where their primary prey can access different depths?

Chapter 6: Why are some little penguins so little: an effect of Ashmole's halo on foraging behaviour?

Appendix

Chapter 1: General Introduction

To maximise reproductive fitness an individual must maximise the energy it obtains from food and minimise the time and effort it spends seeking it (Emlen 1966, MacArthur and Pianka 1966). This thesis explores the nature of the balance between the effort spent seeking food and the energy it provides for offspring and growth. To do this it uses the little penguin *Eudyptula minor* as a model because the foraging, diet and reproductive variables displayed by this species are readily measurable, given that this species can be accessed in colonies throughout the year. In the marine environment, the little penguin also has a wide variety of food, and foraging areas from which to chose, providing a framework in which to investigate how a species maintains this balance.

Central-place foragers

Life history characteristics and environment impose many constraints on how individuals seek energy. For many species, adults are tied to a specific place while breeding because their young are immobile; e.g. at a nest, hive or colony. During breeding, such adults become central-place foragers that are restricted to foraging near the breeding site to provision their young (Orians and Pearson 1979). Central-place foragers, including many carnivorous mammals and birds, generally invest a high level of parental care while their young remain at their central-place (e.g. den or nest) and although their young are few in number, each has a relatively high probability of surviving to adulthood. These are characteristics of 'K-selected' species, which are defined by MacArthur and Wilson (1967) as having individuals that are strong competitors in a crowded niche that is near or at its carrying capacity. Some of these animals are restricted by central-place feeding throughout their lives, because only one place provides food or a food-cache (Barrette and Giraldeau 2008), protection for resting, information transfer or territory (Kacelnik 1984, Kramer 1982, Dornhaus *et al.* 2006). Permanent central-place foragers must therefore ensure that local food is always available or continually replenished.

In contrast, other animals that produce many offspring, such as most fish, typically invest very little in providing for their young, each of which has a relatively low probability of surviving to adulthood. These 'r-selected' species mature early, have a short generation time and their young can disperse widely into less-crowded ecological niches. Consequently their population growth rates are high when and where conditions are favourable (MacArthur and Wilson 1967). These animals may use a central place for a very short period of time (e.g. sea turtles that come to a beach to lay eggs) or not at all (e.g. broadcast spawning fish).

Since Orians and Pearson (1979) galvanised thinking on the limitations that a central-place imposes on foraging, other refinements of central-place foraging theory suggest that different habitats and environmental processes also limit foraging. Habitat types that impose central-place foraging include the surface of the sea for a diving mammal (Lea *et al.* 2002, Staniland *et al.* 2010), ponds for an amphibian (Shakhparonov 2008) or short-grass meadows for white storks (Johst *et al.* 2001). Central-places can also be oceanographic features such as eddies, thermoclines and upwelling systems where pelagic seabirds aggregate to feed (e.g. Becker and Beissinger 2003, Ropert Coudert *et al.* 2009, Kai and Marsac 2010).

There are usually many suitable central-places for both terrestrial and aquatic species because they have expansive habitats. In comparison, some species require two habitats, such as the sea in which to feed and land on which to breed (or vice versa). These species are more restricted in where they can establish a central-place because these places (e.g. islands) are far less common. Examples of such species include seabirds (Dann and Norman 2006), seals (Staniland *et al.* 2010) and land crabs (Adamczewska and Morris 2001). For this reason, these places can become densely populated with central-place foragers, resulting in competition for both breeding space and food (Danchin and Wagner 1997).

Animals that are restricted to central-places typically evolve specialised phenotypes or strategies to exploit local food resources because they cannot move to seek it elsewhere. Readily obtainable measurements of the behaviour of central-place foragers, such as foraging trip duration and distance, residence time and food intake, have been used to determine how animals overcome the constraints of central-place foraging (Kacelnik 1984, Kaspari 1991, Ropert-Coudert *et al.* 2004). Adaptations include the ability to rapidly cover long distances (e.g. albatrosses, Waugh *et al.* 1999) and the ability to carry large or many food items while travelling (e.g. eastern chipmunks *Tamias striatus* with expandable cheek pouches, Kramer 1982). The use of multiple central-places is another adaptation used by spider monkeys *Ateles geoffroyi*, which repeatedly use several sleeping trees in which to sleep and care for young, and they choose the sleeping site closest to their current feeding area (Chapman *et al.* 1989). Other central-place foragers process food into milk (e.g. elephant seals, Galimberti and Boitani 1999), oil (e.g. shearwaters, Warham 1990), or a macerated meal (e.g. penguins) to maximise the efficiency of energy delivery to offspring from distant foraging grounds (Ydenberg 1994, Hamer *et al.* 2002). Young petrels and albatrosses can also store food as oil when their parents are absent for long periods (Hamer *et al.* 2002) and penguins can slow digestion (Wilson *et al.* 1989). These adaptations allow animals to minimise the time or energy they must spend on commuting, searching and handling food, while maximising the food returned to the central-place (Orians and Pearson 1979, Ydenberg 1994, Ropert-Coudert *et al.* 2004, Wilson *et al.* 2005).

Impact of population size at the central-place

While local prey resource levels determine the maximum size of a population, the size of the population at the central-place can influence the strategies that individuals use to exploit nearby food to increase reproductive success. In dense populations, where intra-specific competition for nearby resources is high (Lewis *et al.* 2001), individuals can maximise foraging success and fitness by becoming highly familiar with their foraging areas and using these same areas from year to year (Irons 1998, Watanuki *et al.* 2003, Grémillet *et al.* 2004). Colonial central-place foragers also use sites surrounded by or near reliable food (e.g. productive oceanic fronts, Bost *et al.* 2009). Disadvantages of living in a large colony are that if local conditions deteriorate or contagious diseases are introduced, the entire colony may suffer high mortality and reduced reproductive success (Furness and Monaghan 1987, Dann *et al.* 2000, Tasker *et al.* 2000). In contrast, when only one or two animals forage around a central-place (e.g. a pair of nesting brown falcons *Falco berigora*), competition for food may be minimal (McDonald *et al.* 2003). Unlike large colonies which are usually geographically fixed from year to year, a single pair of birds can choose when and where they breed each year, based on when and where environmental conditions and food availability are most favourable, and on the number of competitors in the vicinity.

The population size at a central-place can also influence strategies for social interaction and predator avoidance. Many central-place foragers such as seals and seabirds benefit from breeding in dense colonies (Hunt 1986, Staniland *et al.* 2010). These individuals benefit because they have increased mate choice (Lewis *et al.* 2001) because they breed at the same time (Drent 2006), and have more opportunities to exchange information about where to find food (Dornhaus *et al.* 2006), as well as more opportunities for creching young (Peron *et al.* 2010). Individuals in large colonies are also exposed to less predation risk due to the dilution effect of many individuals and only a few predators (Hamilton 1971). Further, many individuals keeping watch for predators provide an early-warning effect so that individuals can change their behaviour to avoid predation (Lazarus 1979). Other strategies are used by very small populations at a central-place, such as single pairs of nesting birds. A pair of American robins *Turdus migratorius* nesting alone can more easily avoid detection from predators by choosing to visit their nest less frequently when predation risks (for their young) are high, even at the cost of provisioning young with less food (Johnson and Swihart 1989).

Balancing foraging strategies with reproductive output

Central-place foraging during the breeding season is a trade-off between opposing foraging strategies that benefit parents (foraging to distant and more productive areas) and offspring (having parents return frequently with food) (Ydenberg 1994). Central-place foraging theory suggests that an animal should catch larger prey (for single prey-loaders) or more prey (multiple-prey loaders) further from the central-place where there are fewer competitors (Orians and Pearson 1979). Such returns must outweigh the extra energy required for adults to travel further afield and the energy cost of prolonged fasting of young. Some studies have revealed that parents balance the cost of reproduction with individual maintenance and survival, particularly in long-lived birds such as albatrosses and petrels (Dobson and Jouventin 2010 and references herein). In other words, birds that have evolved to live longer have lower fecundity. They also have lower fledging success because their provisioning rate is slower. The distance from a central-place at which a parent chooses to forage is therefore an individually based compromise. This is the individual optimisation hypothesis of Perrins and Moss (1975). The success of this strategy will depend on the scarcity and/or quality of food near the central-place as well as the foraging skills of the individual. Scarcity of food near the colony may result from several causes: because breeding habitat (e.g. islands for seabirds) is not adjacent to food resources (spawning fish grounds); because intra-specific competition makes foraging inefficient nearer the colony (e.g. for common murres *Uria aalge*, Davoren *et al.* 2003); or because local food becomes depleted over time (e.g. for large colonies of thick-billed murres *U. lomvia*, Elliott *et al.* 2009).

Ashmole's halo

At densely populated colonies, central-place foragers can deplete food around a colony during the breeding season. This phenomenon of prey-depletion in the area surrounding the colony is known as 'Ashmole's halo' (Ashmole 1963, Birt *et al.* 1987, Gaston *et al.* 2007, Elliott *et al.* 2009). The size of the halo where prey is reduced is predicted to increase with the population size of the colony. This is because a large population catching prey near the colony will often cause local depletions faster and more extensively than a small population. The halo is also predicted to be inversely related to reproductive success. As food becomes more difficult to find, young will be provisioned less (Cairns 1989, Gaston *et al.* 2007). When local food is depleted near the colony, adults are forced to forage further away, and for longer periods. This should also be the case if the food abundance is lower in general (not just locally) irrespective of any depletion caused by predation. If the increased energy that is spent on foraging further away does not result in higher foraging success, then the growth and survival of young may be reduced (Santema *et al.* 2009). In dense colonies, growth and survival of young is further reduced by high rates of disease, parasites and adult aggression (Brown and Bomberger-Brown 1996, Danchin and Wagner 1997). Foraging choices and food availability thereby regulate population density in large colonies (Ashmole 1963, Gaston *et al.* 1983, Hunt 1986, Lewis 2001), and may have driven K-selected life-history strategies in colonial marine mammals and seabirds, such as delayed maturity, low fecundity, high breeding success and high adult survival (Gaston 2004, Dobson and Jouventin 2007).

Feeding strategies

Local prey availability, together with the behaviour of prey, also influences foraging choices of central-place foragers (Votier *et al.* 2008, Fort *et al.* 2010) and ultimately defines the feeding strategy of many predators. Generalist and specialist strategies define the extremes of the dietary continuum (Bissett and Bernard 2007, Newbold and MacMahon 2009). Generalists are able to switch or mix food types depending on what foods are most available, making them less sensitive to food fluctuations and environmental change (Blake 1984, Bernays and Minkenberg 1997, Klemola *et al.* 2002, Dupuy *et al.* 2009, Grémillet and Boulinier 2009). Alternately, if one food type is consistently abundant, a species or individual may evolve specialist strategies to target a particular food type, regardless of natural fluctuations in abundance of other available food (Fox and Morrow 1981, Roper 1994, Bolnick *et al.* 2003). For example, Darwin's finches *Geospiza* spp. on different islands and in different populations have evolved different shaped bills; these changes were driven by differences in seed type, shape or size (Grant 2003 and references herein). In other species, such as horned lizards *Phrynosoma* spp. in North America, some subpopulations have developed specialist diets on harvester ants *Pogonomyrmex* spp. (Suarez et al. 2000), while others have become opportunistic generalists (Newbold and MacMahon 2009). Specialists are, however, less common than generalists, probably because, for many species, the costs of specialisation outweigh the benefits (Toft 1995).

The foraging strategies of predators can have different effects on the abundance of their prey. Generalist avian and mammal predators in woodland and farmland habitats can stabilise the populations of multiple prey species (rodents and lagomorphs) by switching to a different prey when the most abundant prey type begins to decline (Dupuy *et al.* 2009). For this reason generalist populations are relatively stable. In contrast, the populations of specialist predators in the same habitats fluctuate with the abundance of their dominant prey. This is because specialist predators do not switch prey and therefore do not have these stabilising effects on their prey (Dupuy *et al.* 2009). The foraging and breeding of specialists such as common guillemots *Uria aalge* and Arctic terns *Sterna paradisaea* are also affected by the abundance, distribution and movement of their preferred prey, sandeels *Ammodytes hexapterus*. These seabirds forage for longer, have poorer reproductive success and delay breeding when sandeel abundance declines (Monaghan *et al.* 1989, Monaghan *et al.* 1992, Wright and Begg 1997). Specialist–prey relationships may be more complex when specialists are nomadic, such as owls and kestrels that are able to move to areas of high prey density (Korpimäki 1985). However, the ecology of central-place specialist foragers can provide indicators of change in prey availability, which is an important tool for managing prey stocks that are also harvested commercially (Monaghan *et al.* 1989, Springer *et al.* 1996, Furness and Camphuysen 1997, Boyd and Murray 2001).

Growth strategies

The foraging strategy of a parent determines the growth and survival of their young. In dependent young, selection favours adaptations of physiology, behaviour and morphology that best minimises the impact of variations in food availability on their survival (Schew and Ricklefs 1998). Central-place foragers typically have extended provisioning periods (Weimerskirch 2009), increased competition for local food (Lewis *et al.* 2001) and have to spend time and effort commuting to foraging areas (Weimerskirch 2007). These constraints can make provisioning infrequent and/or unreliable but there is a range of growth strategies that young employ to adapt to the frequency or size of these meals. Wandering albatross *Diomedea exulans* and king penguin *Aptenodytes patagonicus* chicks grow slowly and remain dependent on their parents for more than a year, so that the effects of food fluctuations on growth are buffered (Weimerskirch and Lys 2000, Oatley *et al.* 2007). While parents are tied to the breeding site for prolonged periods, the high investment is generally reflected in high survival of the young (Weimerskirch 2009). Shearwater chicks become temporarily obese from the infrequent but very large, oil-rich meals their parents deliver following trips to distant regions, such as Antarctica where prey are more abundant (Warham 1990, Riou and Hamer 2010). In contrast, brief parental care periods with frequent provisioning minimises the time that both young and parent are constrained by food conditions near the breeding site (Hamer *et al.* 2002).

Southern elephant seal *Mirounga leonina* pups suckle high-energy milk to triple their mass within a very short parental care period (24 days) (Galimberti and Boitani 1999). Similarly, hooded seal *Cystophora cristata* pups suckle sufficient milk to wean in just four days (Bowen *et al.* (1985). However, brief parental care periods mean that young have limited opportunity to learn survival and foraging skills while their parents are supporting them.

Differences in life history constraints between sexes, has prompted the development of growth strategies such as sexual size dimorphism (SSD). SSD is the difference in the overall body size or size of body parts between males and females of the same species (Krijgsveld *et al.* 1998, Torres and Drummond 1999, McKenzie *et al.* 2007). This is particularly evident in polygamous mammals (McDonald 2002, Isaac 2005) and some birds (Agnew and Kerry 1995, Koffijberg and van Eerden 1995, Müller *et al.* 2005). SSD may reflect intrinsic differences in metabolism, where females direct more energy than males into reproductive development and less into growth (Krijgsveld *et al.* 1998, Beck *et al.* 2003, Isaac 2005). The extent of SSD can be accentuated when food conditions are favourable (Krijgsveld *et al.* 1998, Becker and Wink 2003, Badyaev 2002). In some species that exhibit SSD, such as the common murre *Uria aalge* and brown songlark *Cinclorhamphus cruralis*, parents provision young of different sexes unequally, with the sex that has a higher variance in lifetime reproductive success (males in these species) typically getting more resources. This can result in growth rate differences of the young (Cameron-MacMillan *et al.* 2006, Magrath *et al.* 2007). The implications of this are that in years of poor food availability parents may be less successful in fledging their male young, and/or deplete their own body reserves because males can be more costly to provision (Magrath *et al.* 2007).

Seabirds as model species

The colonial habits of seabirds provide a model system from which to examine foraging ecology of central-place foragers. Seabirds are an interesting group because their land-reliant breeding biology is similar to that of their terrestrial ancestors, thereby creating limitations for their marine lifestyle. Seabirds raise their chicks on land because their young cannot fly, swim or dive until they grow adult feathers.

Provisioning adults forage widely for prey, which they target beneath the surface of the sea. Seabirds are long-lived, with long maturation periods, high adult survival rates, and low reproductive outputs (Weimerskirch *et al.* 1993, Weimerskirch and Lys 2000, Dobson and Jouventin 2007). Most seabirds are also faithful to their breeding sites and foraging areas (Irons 1998, Grémillet *et al.* 2004, Bost *et al.* 2009). These characteristics indicate favouritism towards self-preservation over reproductive success (Lack 1968), and may reflect adaptations that buffer their populations against fluctuations in prey availability (Boyd *et al.* 2006). When prey availability decreases, adults may increase effort such as travelling further for food, abandoning young or provisioning young less, which may come at the cost of reproduction (Monaghan *et al.* 1989).

Physiologically, diving seabirds are restricted in the depth to which they can dive on account of their requirement to breathe air. Flying seabirds are also restricted in the mass with which they can return to provision their chick because increased mass affects the ability to fly. Seabirds that carry single prey in their bills are further restricted by the need to return to their chick after each prey item has been caught (e.g. terns). The constraints that physiology and terrestrial breeding impose on parents' provisioning strategies enable the examination of how their foraging strategies, offspring growth and diet vary in response to changes in prey availability.

Little penguins are resident central-place foragers that remain tied to their colony throughout the year, not just in the breeding season. They visit the colony to moult and breed, and also visit the colony frequently to rest. Because little penguins provision their chicks frequently for a seabird (once every 1-5 days, Chiaradia and Nisbet 2006), they forage relatively close to their colony (usually within 20 km, Collins *et al.* 1999, Bool *et al.* 2007, Preston *et al.* 2007, Hoskins *et al.* 2008) compared with many seabird species, including: albatrosses (Cherel *et al.* 2000, Waugh *et al.* 2000, Waugh *et al.* 2003), shearwaters (Dall'Antonia *et al.* 1995, Peck *et al.* 2008), and white-chinned petrels (Catard *et al.* 2000); all of which forage hundreds of kilometres from their colonies. The majority of little penguin colonies are located on islands where terrestrial predators are absent (Marchant and Higgins 1990, Robinson *et al.* 1996, Brothers *et al.* 2001). It is these islands, together with food resources around them that limit and determine the distribution of colonies, population size of colonies and foraging ranges of the penguins. Little penguins appear to be constrained to foraging on near-shore prey species in shallow coastal waters adjacent to islands (Cullen *et al.* 1992, Chiaradia *et al.* 2003, Lenanton *et al.* 2003.). Little penguins are multiple-prey loaders, which gives them flexibility to forage for the entire day before returning to their chicks at dusk. Diet studies indicate that little penguins are generalist predators that target whichever small schooling prey are abundant near their colony (Klomp and Wooller 1988, Montague and Cullen 1988, Gales and Pemberton 1990, Cullen *et al.* 1992, Chiaradia *et al.* 2003, Eberle 2003). Chick growth is relatively rapid over the 7-9 weeks of parental care, and growth is steady (although sigmoidal) because meals are frequent (Wienecke *et al.* 2000, Chiaradia and Nisbet 2006).

Eastern Great Australian Bight

The eastern Great Australian Bight (GAB) region, together with Spencer Gulf and Gulf St Vincent, is considered relatively isolated from the neighbouring regions to the east and west, on account of the region's unique oceanography, ecology and biogeography, including the distribution of islands (Department of the Environment and Water Resources 2007) (Fig. 1). The region's broad continental shelf waters and gulfs are nourished by seasonal upwelling events in spring and summer to the south of Spencer Gulf (Lewis 1981, Middleton and Bye 2007). The nutrients delivered by upwelling events support primary productivity (van Ruth *et al.* 2010) which attracts a large biomass of small pelagic fish and many apex predators such as whales, seabirds and seals (Page *et al.* 2005, Gill *et al.* 2010, McLeay *et al.* 2010), including little penguins (Bool *et al.* 2007). The clupeoid baitfish in this system include sardine *Sardinops sagax,* which is the target species of the largest volume fishery in Australia. The fishery harvest, mostly centred in southern Spencer Gulf, reached 39,000 tonnes in 2005 and 36,500 tonnes in 2010 (Ward *et al.* 2008, Ward *et al.* 2010). The eastern GAB region is also characterised by having many islands, submarine canyons and two gulfs, which create habitat and shelter for marine organisms (Department of the Environment and Water Resources, 2007). East of this region, the freshwater flows out of the mouth of the Murray Mouth may once have formed a salinity barrier to dispersal of near-shore taxa (Edgar 1986). Although the outflow from the

Murray Mouth is unlikely to pose a barrier to penguins, it may have played a role in facilitating the development of different marine communities to the west (eastern GAB) and south-east.

The life history of little penguins in the eastern GAB differs from that of many little penguins in south-eastern Australia (Victoria, Tasmania, New South Wales) and New Zealand, where most of the species is distributed. In the eastern GAB (where data have been collected from two colonies) as well as in Western Australia, penguins have larger bills and are heavier than those in south-eastern Australia (Overeem *et al.* 2006). In the eastern GAB (and in southern Western Australia), penguins breed during Autumn to Spring (April-November), with peak breeding in winter. They often breed twice in the season (double broods) and moult in early December. In contrast, many penguins in south-eastern Australia and New Zealand breed during spring and summer, and moult in February (Stahel and Gales 1987, Goldsworthy *et al.* 2000, Chiaradia *et al.* 2003, Robinson *et al.* 2005, Miyazaki and Waas 2003, Weerheim *et al.* 2003). Exceptions include colonies in St Kilda (Victoria) and Oamaru (New Zealand) where breeding occurs in winter (Cullen *et al.* 1996, Johannesen *et al.* 2003, Preston *et al.* 2008). In general, the distribution of breeding phenology of colonies in the eastern GAB is relatively early. The colonies in this region are also geographically relatively distant from colonies to the east (Victoria) and west (Western Australia). Most studies on the ecology of little penguins have been conducted in south-eastern Australia, particularly Victoria and Tasmania (Montague and Cullen 1988, Gales and Pemberton 1990, Bethge *et al.* 1997, Collins *et al.* 1999, Dann 2000, Geise *et al.* 2000, Chiaradia *et al.* 2003, Eberle 2003, Robinson *et al.* 2005, Dann *et al.* 2006, Ropert-Coudert *et al.* 2009) and in New Zealand (Bull 2000, Johannesen *et al.* 2002, Miyazaki and Waas, 2003). Why eastern GAB little penguins have developed a different reproductive ecology to that of eastern Australian populations is unclear, but the difference in the timing of breeding is likely to be driven by local adaptations to foraging conditions.

Very few studies have been conducted in the eastern GAB (Bool et al. 2007, N. Gilbert unpubl. data) and a few more have made regional comparisons between the morphology and genetics of penguins across the distributional range of the species

(Overeem *et al.* 2006, Overeem *et al.* 2007, Peucker *et al.* 2009). There is currently limited understanding of how the penguins in the eastern GAB respond to differences in the availability of food and how they may be impacted by current or future fishery harvest. Geographically separated colonies of little penguins in the eastern GAB offer natural experiments to compare and contrast the effect of different foraging conditions on diet, foraging behaviour and growth. Developing a greater understanding of these localised foraging adaptations is a key focus of this study, knowledge of which will underpin future management of penguins in the region.

General Objective and Aims of this Study

The general objective of this study was to describe the functional relationships between the diet, foraging behaviour and chick growth of little penguins in the eastern GAB. Based on previous studies on little penguins in other parts of their range, little penguins in the eastern GAB are hypothesised to:

1. consume small schooling prey that are locally abundant;
2. optimise their foraging behaviour to enhance foraging and reproductive success;
3. show preference for foraging in shallower environments where they can access prey in the water column; and
4. demonstrate regional differences in body morphology that reflect local differences in prey availability.

Specific Aims

To address the general objectives and hypotheses, this study specifically aimed to:

1. Determine inter-sexual and inter-colony variation in body and bill size across age groups and to assess the likelihood that differences can be attributed to regional variation in long-term food availability.

2. Describe the diets of little penguins from colonies in the eastern GAB, and document variation in prey composition, biomass and energy content over years and seasons.

3. Estimate the population size of little penguins at four of the region's largest colonies across the eastern GAB.

4. Estimate the consumption of local prey by little penguins in the region.

5. Describe the foraging behaviour (diving and surface tracks) of breeding little penguins and its variation between colonies and years.

6. Assess the extent to which foraging behaviour responds to changes in environmental conditions, pre-departure body conditions, population size, and prey availability.

Permits and Ethics

Permits and ethics for this research were approved by the South Australian Department for Environment and Heritage. Ethics committees from Primary Industries Research South Australia and The University of Adelaide also provided approval for this work.

Study Sites and the Populations of Little Penguins in this Study

Data for this thesis were collected from eight colonies in the eastern GAB: Troubridge Island (35°07'S, 137°50'E), Reevesby Island (34°32'S, 136°17'E), Greenly Island (34°39'S, 134°46'E), Pearson Island (33°57'S, 134°15'E), Olive Island (32°43'S, 133°58'E), West Franklin Island (32°27'S, 133°39'E), West Island (35°37'S, 138°36'E) and Granite Island (35°33'S, 138°37'E) (Fig. 1). With breeding populations of between 1,800 and 12,000 penguins (this study), these colonies (excluding West and Granite Islands which are smaller) represent some of the largest colonies in the region. Troubridge and Reevesby Islands are located in separate shallow gulfs with a sea-floor depth of < 40 m. Several other seabird species nest on these islands between spring and autumn (including crested terns *Thalasseus bergii* and short-tailed shearwaters *Puffinus tenuirostris* respectively). In summer there appears to be little connective flow between the gulfs, or between the gulfs and shelf systems due to a 'frontal boundary' at the mouth of the gulfs resulting from the density difference between the hyposaline gulf waters and the marine shelf waters outside (Department of the Environment and Water Resources

2007). Therefore these gulfs act as relatively closed marine systems, supporting their own primary productivity. In winter, nutrient-rich water from the shelf flows into these gulfs along their western sides where Troubridge and Reevesby Islands are located (Middleton and Bye 2007).

Greenly, Pearson, Olive and West Franklin Islands are located on the open continental shelf where the seafloor is generally between 30 and 90 m deep. West and Granite Islands are 3 km apart in a wide bay associated with shelf waters, exposed only to the south-easterly oceanic weather. New Zealand fur seals *Arctocephalus forsteri*, which are known to be predators of little penguins (Page *et al.* 2005) haul out at all of these islands. While no other large seabird colonies occur on these islands, thousands of short-tailed shearwaters *Puffinus tenuirostris* and white-faced storm petrels *Pelagodroma marina* nest during the summer on many neighbouring islands. The shelf waters are predominantly influenced by westerly winds during the winter, which force down-welling of waters at the coast thereby suppressing ocean primary productivity (Van Ruth *et al.* 2010). In summer the shelf experiences south-easterly winds, which drive productive coastal up-welling events south of Eyre Peninsula (Van Ruth *et al.* 2010). Austral seasons are referred to in this thesis: autumn (March-May); winter (June-August); spring (September-November) and summer (December-February).

All island sites (except Granite Island) are remote from urban towns and access is difficult, requiring boat transport in fair weather only. No sites except Granite and Troubridge Islands had facilities such as accommodation, power, drinking water or landing infrastructure.

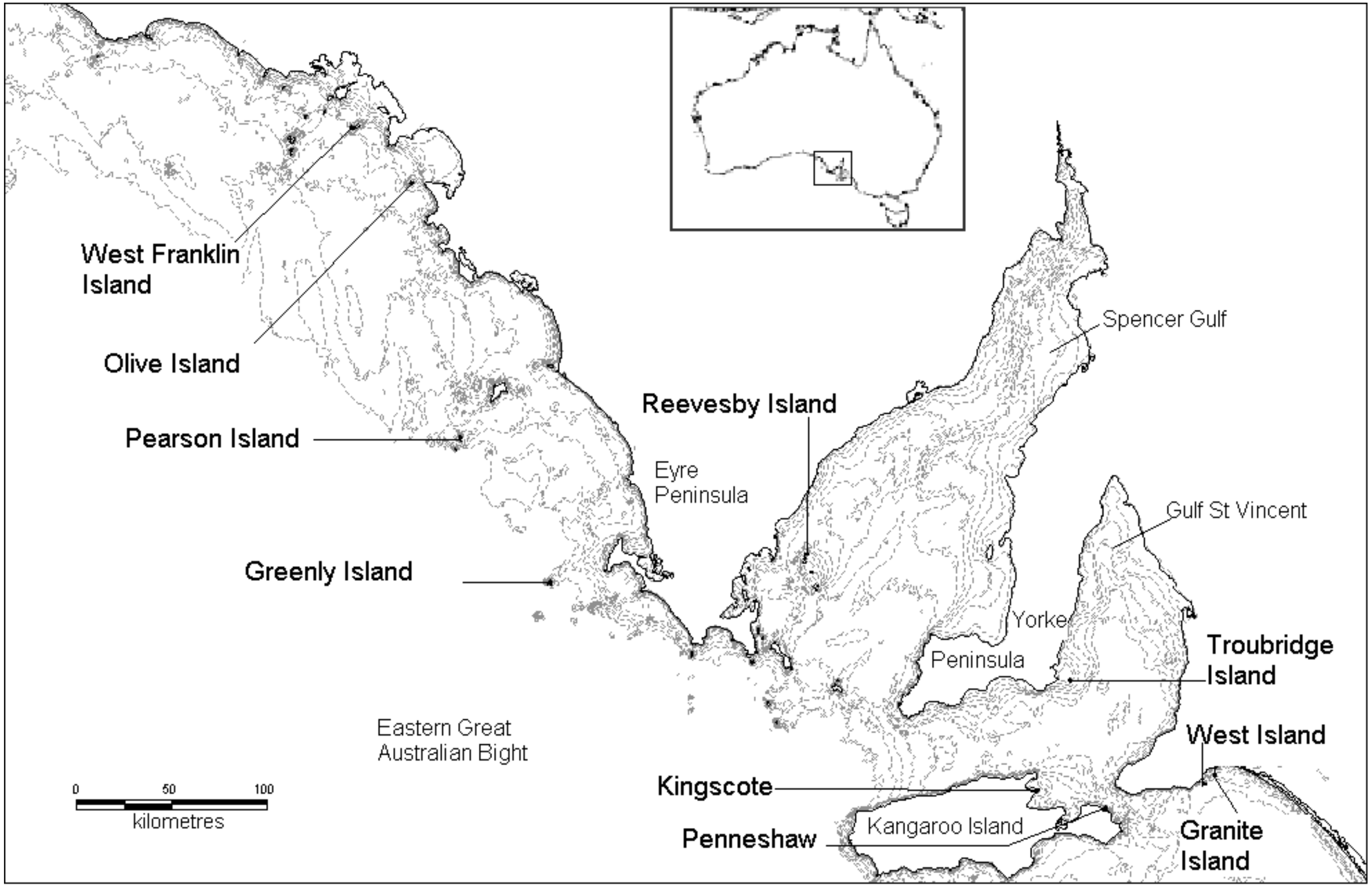

Figure 1. Map of southern South Australia showing the eight little penguin colonies where this study was conducted and others mentioned in this thesis. Insert is Australia with the study region indicated.

Chapters and Organisation of this Thesis

This thesis is a compilation of five papers that are self-contained and therefore some of the introductions, methods and data are duplicated because the content overlaps. Figure and table numbers only refer to the chapter in which they are cited. The one exception is the map in this chapter (Fig. 1.), which is referred to in all other chapters.

Chapter 2 describes and validates the methods used to determine the sex in little penguins at individual colonies using discriminant functions based on bill morphology. Bill morphology also varied between colonies, requiring that I develop colony-specific equations. The determination of the sex of a penguin facilitates ecological comparisons between sexes and is used throughout the thesis. Chapter 3 describes and compares diets of little penguins at eight colonies over a period of three years. This study also determined the relative importance of locally harvested small pelagic fish species and other prey to the timing of little penguin breeding. Chapter 4 details the variation in bill size and sexual size dimorphism in bills and relates it to differences in prey availability. Chapter 5 describes and compares the diving behaviour of little penguins from two colonies where their prey could access different depths. This chapter addresses diving thresholds and whether penguins chose to dive deeper and/or dive more often in deeper water. Chapter 6 compares foraging behaviour of breeding little penguins between four colonies. The findings are discussed with respect to differences in prey availability and body sizes between colonies. Chapter 7 is a general discussion on the variation in the feeding and breeding ecology of little penguins across the eastern GAB. The sensitivity of little penguins to changing prey type or abundances is discussed, together with potential use of little penguins as indicators of environmental change and management implications in the eastern GAB.

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Chapter 2: Determining the sex of little penguins from South Australia using discriminant functions based on bill morphology

Abstract

Many ecological and reproductive studies on seabirds require the determination of sex in adults. The plumage, behaviour and size of male and female little penguins *Eudyptula minor* are very similar. I used measurements of bill depth and length to predict sex in little penguins from two South Australian colonies. Penguins could be sexed using discriminant function analyses with accuracies of 95 % to 100 % for colony-specific subpopulations and up to 92 % across multiple colonies in the region. Colony-specific functions were more accurate than multiple-colony functions, because there were significant differences in adult bill sizes between sites. Functions were appropriate for four other nearby colonies. Discriminant functions developed for colonies in other parts of Australia and New Zealand were less reliable. Regional variation in bill size emphasises the importance of understanding bill variation before using discriminant functions from other regions. Bill depth was also correlated with the depth of foraging areas surrounding colonies, suggesting that the physical environment has influenced differences in bill size.

Introduction

Where there is overlap in the size of male and female seabirds, sexing them can be difficult especially if the sexes are also monomorphic for plumage, vocalisations and behaviour. Because sex determination is integral to many studies, much effort has been expended in overcoming this difficulty. Seabirds have been sexed by cloacal examination (Samour *et al.* 1983), but this method can only be used on females that recently laid an egg. Molecular analyses to determine sex have been used for several seabirds (Bertellotti *et al.* 2002, Constantini *et al.* 2008), but these methods are time consuming and impractical for many studies. Other studies have developed techniques that take advantage of inter-sexual differences in size (Copello *et al.* 2006). To sex adult seabirds, some studies have measured the morphology of a group of known-sex individuals, and calculated sex-specific equations to predict the sex of other individuals (Coulson *et al.* 1983)

A variety of morphometric variables are employed in sex determination of seabirds. The variables include bill and flipper width measurements in Adélie penguins *Pygoscelis adeliae* (Kerry *et al.* 1992), foot length in yellow-eyed penguins *Megadyptes antipodes* (Setiawan *et al.* 2004) and combined head and bill measurements in flesh-footed shearwaters *Puffinus carneipes* (Thalmann *et al.* 2007). Bill depth and to a lesser extent bill length have been used to predict the sex of little penguins *Eudyptula minor* (Gales 1988, Arnold *et al.* 2004). This is because bill depth is the most dimorphic skeletal structure in penguins (Renner *et al.* 1998). Bill variables are stable throughout adulthood (Gales 1987) unlike non-skeletal variables such as body mass that fluctuates with season and stage of breeding (Wiebkin 2010). Discriminant function analysis based on these bill morphometrics has been developed for the subspecies *E. m. variabilis* and *E. m. minor* in New Zealand with accuracies of 95 % (Hocken and Russell 2002) and 98 % (Renner and Davis 1999). Discriminant functions (DFs) for *E. m. novaehollandiae* have also been used in south-eastern Australia, where 91 % of birds were correctly sexed (Arnould *et al.* 2004).

Equations that predict the sex of birds have been used among different little penguin colonies in south-eastern Australia (Gales 1988, Arnould *et al.* 2004). Arnould *et al.* (2004) showed that one equation worked well for penguins from

Tasmania (Gales 1988) and Victoria because there was little variation in bill depth. However, considerable variation exists between the bill dimensions of penguins from Western Australia and those in south-eastern Australia (Gales 1988, Klomp and Wooller 1988). For this reason, there is a perceived inadequacy in the reported equations for sexing little penguins, specifically, in South Australia. Very few studies have been done on penguin morphology in South Australia (Overeem *et al.* 2006), a region that lies in the middle of the distribution range of little penguins. This study endeavours to refine sexing methodology for specific colonies within this region.

The aim of this study was to develop separate sex-predicting DFs for two colonies in South Australia and also for both colonies together, to provide regional-based equations. The DFs were used to assess the merits of using colony-specific versus regional-based equations. Based on the low bill morphometric variation found between south-eastern Australian colonies (Arnold *et al.* 2004), I hypothesised that variation would also be low between South Australian colonies and that a regional DF would be appropriate to determine gender across multiple colonies. The DFs developed in this study were compared with those previously developed in other parts of Australia and New Zealand. Differences between penguin bill sizes from coastal and off-shore colonies, also encouraged me to investigate whether there was a link between bill size and water depth around colonies, on the understanding that there may be a difference in the types of prey or ease of capturing prey in different conditions that is related to bill size.

Methods

The study was conducted between 2004 and 2006 on the following islands in South Australia: Troubridge (35°07´S, 137°50´E), Pearson (33°57´S, 134°15´E), Reevesby (34°32´S, 136°17´E), Greenly (34°39´S, 134°46´E), Olive (32°43´S, 133°58´E) and West Franklin (32°27´S, 133°39´E) Islands (Fig. 1 in Chapter 1). These sites are representative of the range of potential sites that penguins could use in the eastern Great Australian Bight (GAB). Coastal sites surrounded by shallow water include Troubridge, Reevesby, Olive and West Franklin Islands. Greenly and Pearson Islands are located further offshore and are surrounded by deeper water.

Morphometric measurements were made on the bills of little penguins during the breeding seasons (May-September) when males and females within a breeding pair could be distinguished. Within pairs the male has a larger bill (Gales 1988, Arnould *et al.* 2004, Hocken and Russell 2002). To identify penguins in breeding pairs, they were tagged with subcutaneously implanted glass-encapsulated TIRIS^{TM} (Texas, USA) transponders, and were recorded at least five times with the same partner in the nest during the season. Bill depth (vertical bill thickness at the nares) (*BD*) and bill length (length of the exposed culmen) (*BL*) were recorded using digital callipers (± 0.01 mm). To test the accuracy of measurements, 10 measurements of *BD* and *BL* were made on four penguins of known sex. One person made all measurements (AW).

A number of data sets were used in this study:

- 3 *reference* data sets (from Troubridge Island, Pearson Island and both islands)
- 3 *test* data sets (from Troubridge Island, Pearson Island and both islands)
- 1 additional *test* data set (Pearson Island, sex confirmed by necroscopy)
- 4 additional data sets (from Reevesby, Olive, West Franklin, Greenly Islands)
- 1 data set of mean bill sizes from 14 colonies across the species' distribution

Three data sets of bill measurements from penguins of known sex were used as *reference* data sets. From these data sets, discriminant functions (DFs) were developed that could then be used to predict the sex of other penguins. Two of the *reference* data sets consisted of measurements from Troubridge and Pearson Islands respectively, with equal numbers of males and females in each. They were used to develop DFs for the respective colonies. A third *reference* data set consisted of an equal number of measurements from both colonies together, hereafter labelled "combined" data set. This combined *reference* data set was used to develop DFs for the region. To ensure sample numbers from both colonies were equally represented in this data set, some of the measurements from Pearson Island were randomly removed.

The *reference* data sets were analysed using a forced-entry discriminant function analysis (SPSS Inc. V16.0, Chicago), which calculates equations that can be used to predict sex. Discriminant function analysis indicates variation in a sample of bill morphometrics by showing the proportion of individuals that are allocated to the correct sex. Two DFs were developed for each of the Troubridge and Pearson Islands and combined *reference* data sets, one using BD and *BL,* and the other only *BD*. The precision of the groupings was verified through cross-validation.

For each *reference* data set (Troubridge and Pearson Islands and combined), the values for correlation matrices were less than 0.7, indicating that no multi-collinearity existed between the variables (Zar 1984). Kolmogrov-Smirnov and Levene's tests were used to ensure that all sex-specific data sets were normally distributed and had equal variance with an α level of 0.05 to test for significance. Unless stated otherwise, discriminant scores (DS)*,* which assigned individuals to a sex, were separated at 0 (cut-off value) and negative DS indicated females and positive DS indicated males. The DFs were then tested on three *test* data sets of bill measurements from other little penguins (not those in the *reference* data sets) of known sex (from Troubridge and Pearson Islands, and equal numbers combined together respectively). Additional bill measurements from dead little penguins (necropsied to confirm their sex) were also used to test DF accuracy. Results were reported in ranges and means ± S.E. (mm).

Bill measurements from four other nearby colonies; Reevesby, Greenly, West Franklin and Olive Islands (Fig. 1 in Chapter 1) were used to further investigate the variation in *BD* and *BL* across the region. The combined DF based on *BD* and *BL* (from Troubridge and Pearson Island measurements) was used to predict sex at these four colonies. The resulting DS for each sex were compared with those of the combined data set to determine whether the DFs developed in this study was appropriate for sexing penguins from these other nearby colonies. To determine whether geographic variation across much of the species distribution range affects the accuracy of DFs, I applied the DFs developed for little penguins in south-eastern Australia and New Zealand to my *reference* data set.

Penguins are known to dive to deeper depths when deeper water exists (Chiaradia *et al.* 2007) where there may be different prey that might be related to bill size.

Alternatively because bill size is reflected in body mass (mean bill size (mm)/ mean body mass (g) = 0.01 at each of six colonies; Chapter 6), penguins with larger bills may dive to different depths than those with smaller bills. To investigate whether water depth is correlated to bill morphology, mean *BD* and *BL* of male and female little penguins from 14 colonies across the species distribution were compared with the mean and median bathymetry of each colony's available foraging area. Mean bathymetry was determined from the average depth of 1 minute-grid cells (GEBCO world bathymetry: www.bodc.ac.uk) within the 20 km radius of ocean surrounding each colony, which encompasses the foraging range of breeding little penguins (Collins *et al.* 1999, Bool *et al.* 2007). Charts of South Australian coastal regions (AUS345 Gulf of St Vincent and approaches, and AUS342 Streaky Bay to Whidbey Isles) were also consulted to validate water depths.

Results

Developing discriminant functions to predict sex

Measurement accuracy was high because within each set of 10 bill measurements of the four different penguins, measurements varied less than 0.14 mm either side of the mean for *BD* (1.4 % of mean) and *BL* (0.4 % of mean). For the *reference* data sets, bill measurements were recorded from 114 penguins at Troubridge Island and 226 penguins at Pearson Island. Males were larger than females for *BD* and *BL* in all data sets (Table 1).

Table 1. Means and ranges of bill depths (*BD*) and bill lengths (*BL*) (mm) for male (M) and female (F) little penguins in the Troubridge Island reference data set (females $n = 57$, males $n = 57$), Pearson Island reference data set (females $n = 111$, males $n = 115$), combined reference data set (females $n = 114$, males $n = 114$), and the Troubridge Island test data set (females $n = 16$, males $n = 16$), Pearson Island test data set (females $n = 76$, males $n = 76$) and combined test data set (females $n = 32$, males $n = 32$). (** $P < 0.001$, * $P < 0.05$).

		Troubridge Island			Pearson Island			Combined		
	Sex	Mean ± SE	Range	F	Mean ± SE	Range	F	Mean ± SE	Range	F
Reference data set										
BD	F	13.11 ± 0.08	11.60 – 14.30	322**	12.17 ± 0.05	11.13 – 13.68	759**	12.63 ± 0.07	11.32 – 14.30	449**
	M	15.31 ± 0.09	13.93 – 16.91		14.21 ± 0.05	12.92 – 15.71		14.81 ± 0.07	13.38 – 16.91	
BL	F	38.34 ± 0.19	34.46 – 41.59	33**	37.03 ± 0.14	33.30 – 40.54	135**	37.67 ± 0.15	33.30 – 41.59	95**
	M	39.94 ± 0.21	36.72 – 43.31		39.30 ± 0.17	35.44 – 44.15		39.65 ± 0.14	36.64 – 44.15	
Test data set										
BD	F	13.14 ± 0.16	11.81 –14.30	115**	12.23 ± 0.06	11.15 – 13.51	418**	12.85 ± 0.12	11.79 – 14.13	128**
	M	15.58 ± 0.17	14.42 – 16.42		14.22 ± 0.07	12.92 – 15.71		15.03 ± 0.16	13.38 – 16.42	
BL	F	38.27 ± 0.37	36.11 – 40.61	5*	37.08 ± 0.16	34.52 – 40.49	60**	37.88 ± 0.27	34.93 – 40.61	14**
	M	39.53 ± 0.41	37.69 – 43.45		39.01 ± 0.19	35.44 – 44.15		39.42 ± 0.31	36.64 – 44.15	

The discriminant functions determined for each *reference* data set are presented in Table 2. The distributions of discriminant scores showed that the least overlap between males and females was within the Troubridge and Pearson Island *reference* data sets, with slightly greater overlap in the combined *reference* data sets (Fig. 2a-c). Cross-validation of the DFs verified sex within the Troubridge and Pearson Island *reference* data sets with accuracies > 95.6 % (Table 2). The prediction of sex was less accurate in the combined *reference* data set (> 90.4 % to 91.2 %; Table 3). The DFs based on *BD* and *BL* were generally more accurate than the DFs that used just *BD*. The DFs based on *BD* alone allocated males as penguins with bill depths > 14.22 mm for Troubridge Island, > 13.20 mm for Pearson Island and > 13.71 mm for the combined data set. DFs based on *BL* alone were largely inaccurate.

Table 2. The discriminant functions used for allocating sex to adult little penguins at Troubridge Island, Pearson Island and at either colony (combined). Eigenvalues and Wilks' λ presented. $P < 0.001$ for all discriminant functions. Sex was allocated as male if the DS was greater than the cut-off value and female if it was less the cut-off value.

Colony	Measurements used	Discriminant function equation	Eigenvalue	Wilks' λ	Cut-off
Troubridge Is.	*BD* and *BL*	$DS = -21.919 + (1.527 \times BD) + (0.005 \times BL)$	2.878	0.258	0
Troubridge Is.	*BD*	$DS = -21.762 + (1.531 \times BD)$	2.878	0.258	0
Pearson Is.	*BD* and *BL*	$DS = -28.134 + (1.664 \times BD) + (0.161 \times BL)$	3.583	0.218	-0.034
Pearson Is.	*BD*	$DS = -23.673 + (1.793 \times BD)$	3.389	0.228	-0.010
Combined	*BD* and *BL*	$DS = -19.266 + (1.236 \times BD) + (0.060 \times BL)$	2.002	0.333	0
Combined	*BD*	$DS = -17.639 + (1.286 \times BD)$	1.987	0.157	0

Table 3. The percentage of adult little penguins that were correctly sexed by discriminant functions based on *BD* and *BL*, and just *BD* in the reference and test data sets. Sample sizes are in parentheses.

Data set	Troubridge Island		Pearson Island		Combined	
Reference	*BD* and *BL*	*BD*	*BD* and *BL*	*BD*	*BD* and *BL*	BD
Female	96.5% (57)	96.5% (57)	97.3% (111)	97.3% (111)	90.4% (114)	90.4% (114)
Male	94.7% (57)	94.7% (57)	97.4% (115)	95.7% (115)	92.1% (114)	90.4% (114)
Total	95.6% (114)	95.6% (114)	97.3% (226)	96.5% (226)	91.2% (228)	90.4% (228)
Test						
Female	100% (17)	100% (17)	96.1% (77)	94.8% (77)	99.1% (34)	99.1% (34)
Male	100% (15)	100% (15)	94.7% (75)	97.33% (75)	93.3% (30)	90.0% (30)
Total	100% (32)	100% (32)	95.4% (152)	96.1% (152)	92.2% (64)	90.1% (64)

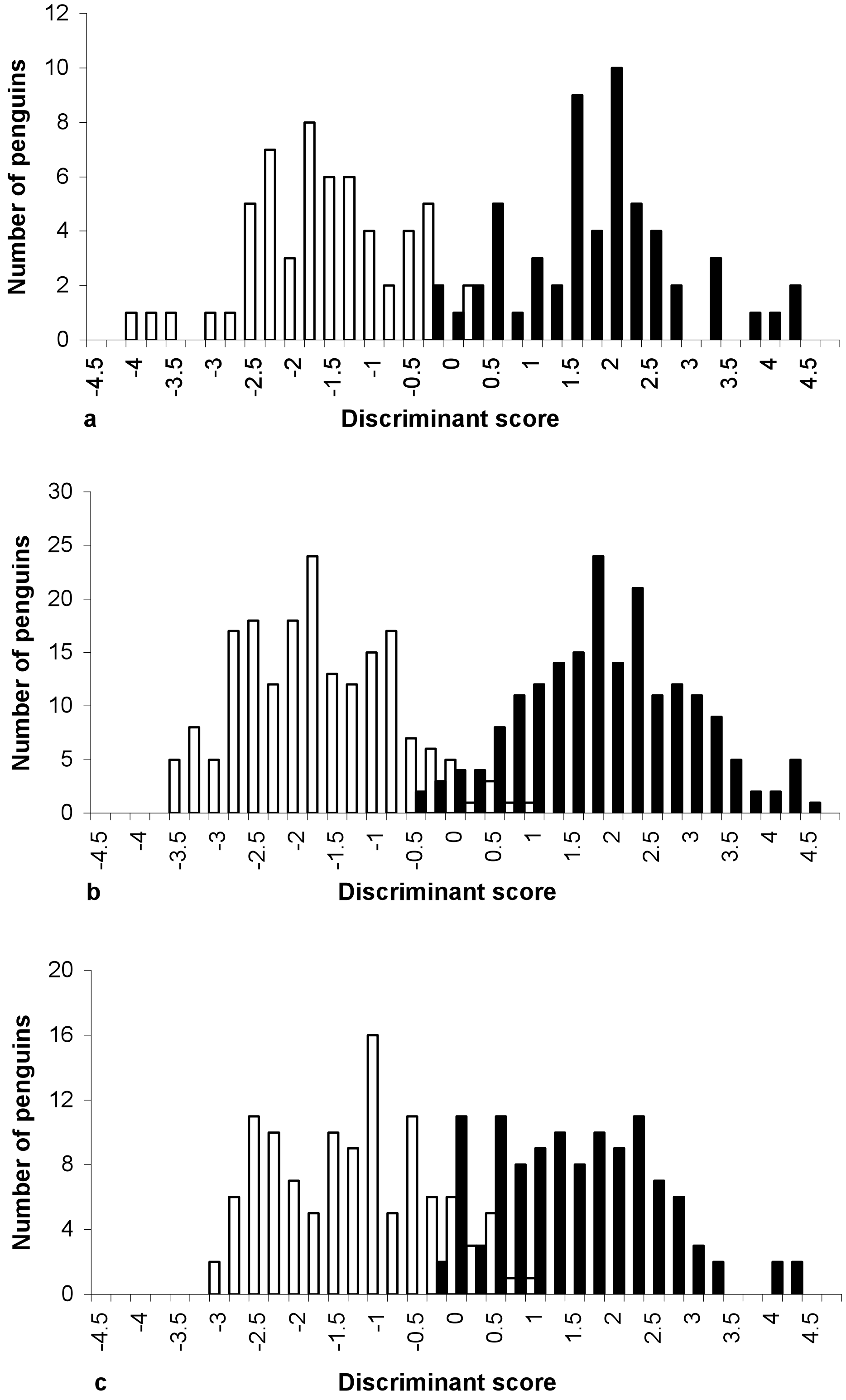

Figure 2. Frequency distributions of discriminant scores for male (black) and female (white) little penguins in the (a) Troubridge Island, (b) Pearson Island and (c) combined *reference* data sets using discriminant functions based on *BD* and *BL*.

Testing discriminant functions to predict sex

The *test* data sets consisted of 32 and 152 little penguins from Troubridge and Pearson Islands respectively. The combined *test* data set comprised 32 randomly chosen individuals with known sex from each site. When the DFs based on 1) *BD* and *BL* together, and 2) *BD* alone, were applied to the respective *test* data sets, sex was predicted with similar accuracies (90.1 % to 100 %) to that achieved in the cross-validation of the *reference* data set (Table 3). When the Pearson Island DF based on *BD* and *BL* together was applied to the Troubridge Island *test* data set, all of the males were classified correctly, but only 56 % females were classified correctly. When the Troubridge Island DF based on *BD* and *BL* together was applied to the Pearson Island *test* data set, only 50 % males were classified correctly, but all of the females were classified correctly.

Fifteen dead adult penguins were found in the Pearson Island colony and their sexes were confirmed by autopsy (Camphuysen 1995). The two Pearson Island DFs correctly sexed all these dead penguins, which included 3 females (*BD* mean = 12.28 ± 0.35 mm, *BL* mean = 36.81 ± 1.24 mm) and 12 males (*BD* mean = 14.38 ± 0.22 mm, *BL* mean = 40.72 ± 0.39 mm).

Using DF in other nearby colonies

Bill depth and length of adults of unknown sex were measured from Reevesby, Greenly, West Franklin and Olive Islands (other islands in the eastern GAB). I assumed that these penguins came from the same broader regional population, as those from Pearson and Troubridge Island. The combined DF based on both *BD* and *BL* together (developed from measurements from Pearson and Troubridge Island together), was applied to these four colonies to assign a sex to individuals and to determine the variation in *DS* across the region. Average *DS* values (positive) for assigned males, from Reevesby (1.11 ± 0.09, n = 79), Greenly (1.12 ± 0.22, n = 19), West Franklin (0.67 ± 0.08, n = 17) and Olive (1.10 ± 0.19, n = 8) Islands did not vary significantly between colonies (F = 1.67, P = 0.181). The average *DS* values (negative) for assigned females from the respective colonies did not vary either (-1.46 ± 0.08, n = 47, -1.40 ± 0.21, n = 11, -1.35 ± 0.21, n = 10 and –1.28 ± 0.19, n = 9) (F = 0.119, P = 0.949). There were also no differences between assigned male and female *BD* and *BL* from each of the four colonies (Table 4) and those from the combined *reference* data set (*F* = 0.88 - 1.38, *P* = 0.11 - 0.75).

Table 4. The mean bill depths and bill lengths mm ± SE of little penguins from Reevesby, Greenly, West Franklin and Olive Islands for each sex as determined by the combined DF based on *BD* and *BL*.

Colony	Sex	*n*	*BD*	*BL*
Reevesby Island	M	47	14.56 ± 0.08	40.86 ± 0.25
	F	79	12.57± 0.07	38.51 ± 0.17
Greenly Island	M	11	14.54 ± 0.18	40.30 ± 0.42
	F	19	12.58 ± 0.16	38.60 ± 0.41
West Franklin Island	M	10	14.24 ± 0.07	39.02 ± 0.28
	F	17	12.69 ± 0.17	37.21 ± 0.40
Olive Island	M	9	15.56 ± 0.15	39.42 ± 0.37
	F	8	12.69 ± 0.15	38.30 ± 0.54

When the *DS* from all six colonies (including Troubridge and Pearson Islands) were compared, least significant differences tests showed that males from Troubridge Island were larger than those at all other colonies and males from Pearson Island were also smaller than those from Reevesby Island (*P* < 0.001 in all cases). Females from Troubridge Island were significantly larger than all others except Reevesby Island, and females from Pearson Island were smaller than all other females (*P* < 0.01 in all cases).

Comparing the use of published DF

The previously published DFs predicted sex in my *reference* data sets with varying degrees of accuracy from 52.7 % to 96.9 % (Table 5.). No published DFs were better at predicting sex for penguins at Troubridge and Pearson Islands than my colony-specific DFs. In all cases tested in this study, one sex was better discriminated than the other. Troubridge females were poorly predicted by the DF developed for south-eastern Australia (54.4 % accuracy using Gales 1988, and 75.4 % using Arnould *et al.* 2004), compared with those developed for New Zealand penguins (100 % using Renner and Davis 1999, and 89.5 % using Hocken and Russell 2002). In contrast, Pearson females were discriminated well by all previously published DFs (97.3 % to 100 %) due to their small bills, whereas Pearson males were relatively poorly identified by the two New Zealand DFs (7 % and 61 %).

Table 5. The proportions of little penguins in each *reference* data set that were correctly sexed using DF from published studies. Male DS > 0, except Renner and Davis (1999).

			Gales (1988)	Renner and Davis (1999)	Hocken and Russel (2002)	Arnould *et al.* (2004)
Reference data sets	Sex	*n*	$DS = -83.10 + (10.06 \cdot \ln BL) + (17.99 \cdot \ln BD)$	$DS = 1.245 \cdot BD + 0.202 \cdot BL - 26.459$ (Male $DS > 0.311$)	$DS = -4.59116 + 0.230657 \cdot BD + 0.034646 \cdot BL$	$DS = 1.242 \cdot BD - 16.774$
Troubridge	F	57	54.4 %	100 %	89.5 %	75.4 %
	M	57	100 %	63.2 %	98.3 %	100 %
	Total	114	77.2 %	81.6 %	93.9 %	87.7 %
Pearson	F	77	97.3 %	100 %	100 %	99.1 %
	M	75	96.5 %	7.0 %	61.7 %	84.4 %
	Total	152	96.9 %	52.7 %	80.5 %	91.6 %
Combined	F	114	75.4 %	92.1 %	94.7 %	86.8 %
	M	114	98.3 %	33.3 %	83.3 %	95.6 %
	Total	228	86.8 %	62.7 %	89.0 %	91.2 %

Bill depth and surrounding water depth

There was a weak but significant negative correlation between mean bill depths of little penguins and the depth of waters surrounding colonies. Female bill depth negatively correlated with both median water depth ($r^2 = 0.36$, $P = 0.023$),) and mean water depth ($r^2 = 0.32$, $P = 0.034$), using Pearson correlation coefficients. Male bill depth correlated with median water depth ($r^2 = 0.28$, $P = 0.049$) and approached a significant correlation with mean water depth ($r^2 = 0.25$, $P = 0.065$). The mean bill depth of both sexes together also correlated with median ($r^2 = 0.34$, $P = 0.030$) and mean water depth ($r^2 = 0.3$, $P = 0.041$, Table 6).

Table 6. The mean *BD* mm for male and female little penguins at 14 colonies and the mean bathymetric depth (m) of the marine areas within a 20 km radius of each colony.

Colony	Water depth m		*BD* mm		Reference
	Mean	Median	Female	Male	
Troubridge Is.	20	20	13.11	15.31	This paper
Pearson Is.	61	70	12.17	14.21	This paper
Reevesby Is.	20	20	12.57	14.56	This paper
Olive Is.	28	30	12.70	14.56	This paper
Greenly Is.	68	75	12.58	14.54	This paper
West Franklin Is.	27	25	12.69	14.24	This paper
Phillip Is.	33	35	12.24	14.36	Arnould *et al.* (2004)
Gibson steps	42	45	12.49	14.54	Arnould *et al.* (2004)
Tiritiri Matangi Is.	14	10	13.30	15.00	Miyazaki and Waas (2003), *BD* from 'middle elevation' group
Oamaru	16	10	13.42	15.71	Hocken and Russell (2002)
Albatross Is.	13	10	12.4	14.5	Gales (1988)
Marion Bay	41	40	12.4	14.3	Gales (1988), Location from Arnould *et al.* (2004)
West Is.	34	40	12.48	14.14	N. Bool (unpubl. data)
Granite Is.	23	25	12.85	14.98	N. Bool (unpubl Data)

Discussion

Sexing adult little penguins by one or two bill measurements is a simple, relatively accurate method that can be used in the field, especially if colon-specific criteria are generated. Molecular analysis of DNA to sex seabirds is 100% accurate (O'Dwyer *et al.* 2006), but this method of sexing cannot be done in the field and is time consuming. The cloacal examination technique (Samour *et al.* 1983, Boesma and Davies 1987, O'Dwyer *et al.* 2006), which requires inspection of a bird's cloacal dilation following egg laying, is not so useful for little penguins because they do not synchronise their egg laying (Fortescue 1995). For these reasons, sexing little penguins by morphometric measurements will continue to be a commonly used technique, so the continued development and testing of this method across multiple colonies is warranted.

Sexual size dimorphism in little penguin bill morphology means that discriminant functions can be used to predict the sex of penguins in South Australia. Other studies have found that bill depth is the most dimorphic skeletal structure in penguins, including gentoo *Pygoscelis papua ellsworthi* (Renner *et al.* 1998) and chinstrap *Pygoscelis antarctica* (Minguez *et al.* 2001). The DFs I developed for little penguins based on *BD* provides a practical method of determining sex in the field, because only one measurement is required. However, the DFs based on both bill depth and length measurements were more accurate and would be recommended. This study developed DFs for adult penguins and the use of adult DFs to predict the sex of juveniles is not known. The bills of little penguin fledglings continue to grow until they become adults at 2 to 3 years of age (Gales 1987, Wienecke *et al.* 2000) and consequently there must be considerable bill size variation amongst juveniles of unknown age. Molecular analysis of DNA remains a good option for sexing juveniles and chicks, particularly where no bill size dimorphism is apparent (Renner and Davis 1999).

The DFs developed in this study predicted sex within colonies with high accuracies, which were similar to those of other colony-specific DFs (Gales 1988, Renner and Davis 1999, Hocken and Russell 2002, Arnould *et al.* 2004, Overeem *et al.* 2006). The combined DF (based on *BD* and *BL*) for little penguins on Troubridge and Pearson Island was also useful for predicting sex in birds from Reevesby, Greenly, West Franklin and Olive Islands (each ~50-500 km from one another) because the variation in bill measurements for each sex was similar to those of the combined *reference* data set. In contrast, when the DFs from Troubridge Island were applied to individuals from Pearson Island and vice versa, they were less accurate in predicting the sex of birds, indicating that the proximity of islands (~350 km) does not imply similarity in morphology.

The large variation in the ability of published DFs to predict the sexes in my *reference* data sets correctly was similar to the findings of Arnould *et al.* (2004). Arnould *et al.* (2004) reported that DFs based on little penguins from New Zealand correctly designated sex in penguins from south-eastern Australia in only 50-85% of cases. Interestingly the best previously developed DF for correctly assigning sex at Troubridge Island was from New Zealand (Hocken and Russel 2002), because penguins from both colonies have large bills.

Bill depth and bathymetry

The correlations between bill depth and the depth of the surrounding waters indicate that DFs built from data collected on little penguins experiencing similar water depths may be more appropriate to use for those colonies. This study provides some evidence to suggest that little penguins with large bill depths (and therefore large bodies; Chapter 3 and Chapter 6) forage in shallow habitats that are similar in depth to little penguin mean dive depths (up to 13 m, Chiaradia *et al.* 2007). Chiaradia *et al.* (2007) also found that penguins dived deeper when the foraging habitat around their colony was deeper. Benthic diving to a shallow seafloor provides important prey capture opportunities (Ropert-Coudert *et al.* 2006), which may benefit chick provisioning rates and growth, including bill growth. The shallow foraging area surrounding Troubridge Island (20 m in depth) compared with Pearson Island (61 m in depth) suggests that penguins from Troubridge Island consistently had better access to different, or more accessible prey, which may have resulted in their development of larger bodies. One may speculate that penguins that are consistently required to forage in deeper water may benefit energetically by being smaller, allowing them to forage more efficiently. I hypothesise that the physical environment, or the way that the physical environment affects food availability influences variation in little penguin bill depth, rather than being genetically determined. Recent work on the sizes of fledglings from Troubridge and Pearson Islands agrees with this notion, because shallow environments with higher food availability support larger fledglings and adults (Chapter 3).

Given that bill size appears to be correlated (although weakly) with depth of foraging area, one might also expect that the strong differences in bill dimensions between males and females infer that the sexes forage in different areas or dive to different depths. Alternatively, the two sexes may be capable of foraging at deeper depths, but differences in foraging behaviour may lie in the costs to do so. Such segregation of foraging areas between sexes can reduce inter-specific competition, which is a particularly valuable strategy for large populations that forage near their colonies (Koffijberg and van Eerden, 1995, Ishikawa and Watanuki, 2002).

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Chapter 3: Do inter-colony differences in the morphology of little penguins result from differences in food availability?

Abstract

I studied the bill morphology of little penguins *Eudyptula minor* to determine inter-sexual and inter-colony differences in their growth patterns at Troubridge and Pearson Islands, South Australia. Sexual dimorphism in adult bill morphology was evident at both sites (bill length and depth were significantly bigger in males), and penguins from Troubridge Island had larger bills. Inter-colony differences were also apparent in the bill morphology of fledgling penguins, and these patterns were consistent with inter-colony differences observed in adults. At Pearson Island, the morphology of fledgling bills was uni-modal in distribution, indicating that male and female fledglings did not differ in bill morphology at this stage of development. At Troubridge Island, the morphology of fledgling bills was bimodal, suggesting that males developed larger bills than females before fledging. I showed that food availability at Troubridge Island was greater than at Pearson Island, which may account for the inter-colony differences in the sizes of males and females. My findings suggest that inter-sexual differences in bill morphology become apparent earlier at sites with more optimal food availability, and that these inter-sexual differences become more pronounced (or develop further) after fledging. Early development of inter-sexual bill size differences may be a result of unequal parental provisioning in favour of male chicks when food is abundant.

Key words: *Eudyptula*; penguin; size; growth; sexual dimorphism; natal philopatry.

Introduction

Foraging ability and food availability dictate foraging success, which determines the amount of energy individuals can set aside for growth and reproduction. The strategies that individuals employ to allocate their limited resources are subject to phylogenetic constraints, which can differ according to the age and sex of individuals (Torres and Drummond 1999, Badyaev 2002, McKenzie *et al.* 2007). Differences in the growth and morphology of individuals of a single species can be inherited (Price and Grant 1984, Barbraud *et al.* 1999) but they can also evolve in response to regional differences in prey type, size and availability, sometimes creating morphologically distinct subpopulations (James 1983, Cooch *et al.* 1991, Grant and Grant 1993, Merila and Wiggins 1995, Ruiz *et al.* 1997). When food is relatively poor, animals such as birds and mammals may grow relatively slowly and/or attain sexual maturity later, and produce smaller offspring (Cooch *et al.* 1991, Arnould and Warneke 2002).

Food availability not only influences growth rates of the individuals at the subpopulation level but also life history growth strategies such as sexual size dimorphism (SSD) within subpopulations. SSD eventuates from differential parental investment (energy and food) or from inter-sexual difference in how energy is allocated, where one sex grows larger than the other (Davis and Speirs 1990, Guinet *et al.* 1999, Magrath *et al.* 2007). Sexual size dimorphism is apparent in many species, but it is particularly common in birds (Andersson *et al.* 2003, Cameron-MacMillan *et al.* 2006, Magrath *et al.* 2007) and polygamous mammals (Isaac 2005). SSD is typically male-biased and it is thought to have evolved through female mate choice of larger males and/or through male competition for resources, breeding space and/or females (Brunner 1998, Isaac 2005, Moody *et al.* 2005, McKenzie *et al.* 2007). Other factors such as population density, temporal, spatial or behavioural sexual segregation of activities, food scarcity and the amount of energy allocated to produce eggs or sperm also influence the degree of SSD (Clutton-Brock *et al.* 1987, LeBlanc *et al.* 2001, McDonald 2002). Sexual dimorphism may allow each sex to exploit different food resources thereby reducing competition when food is limiting, which may reduce competition for seabirds that nest in and forage around colonies (Koffijberg and van Eerden 1995, Ishikawa and Watanuki 2002).

In some species that exhibit SSD, parents provision young of different sexes unequally, with the sex that has a higher variance in lifetime reproductive success typically getting more resources. This unequal provisioning can result in growth rate differences of the young (Magrath *et al.* 2007). In polygamous species, such as seals, biased parental investment to male pups is beneficial because males typically grow up to have a higher variance in lifetime reproductive success as they may sire the offspring of many females, or none (Goldsworthy 2006). Many birds also exhibit SSD despite being mostly monogamous, in which case males and females have equal chances of parenting one clutch per season. For this reason, one would expect monogamous birds to provision their chicks of both sexes equally, as reported in the marsh harrier *Circus aeruginosus*. In this harrier species SSD results from intrinsic differences in growth and/or metabolic rates (Krijgsveld *et al.* 1998). However, in some seabird species, such as cormorants and penguins, male parent condition or size may still have greater influence than female parents on chick growth or fledging success (Ishikawa and Watanuki 2002, Miyazaki and Waas 2003, Robinson *et al.* 2005). Preferential provisioning of male young may therefore be beneficial, as has been found in other monogamous seabirds including common murres *Uria aalge*, which exhibit slight SSD (Cameron-MacMillan *et al.* 2006). For other species including common terns *Sterna hirundo*, a bias in parental provisioning or differential growth rates occurs only in years when food availability is optimal (Becker and Wink 2003, Schauroth and Becker 2008). Sex-specific sibling competition may also influence the extent of SSD in young birds (Müller *et al.* 2005).

The colonial lifestyle of little penguins *Eudyptula minor* facilitates investigation of how growth strategies differ between colonies and sexes and how growth may be affected by food availability. Breeding adult little penguins regularly return to their colony and are restricted by the available prey within their relatively small foraging range of 20 km (Collins *et al.* 1999, Bool *et al.* 2006). Like Magellanic *Spheniscus magellanicus* (Boesma and Stokes 1995) and yellow-eyed penguins *Megadyptes antipodes* (van Heezik and Davis 1990) (the latter in seasons of extreme food shortage), food availability in little penguins is an influential factor in seasonal or inter-annual variation in chick growth (Wienecke *et al.* 2000, Chiaradia and Nisbet, 2006, Ropert-

Coudert et al. 2009, Saraux *et al.* 2011). Few studies, however, have investigated the effects of long-term (multi-year) food availability, or parents' foraging performance as a surrogate for food availability on morphology at the population level (Cooch *et al.* 1991).

Relative to other growth parameters such as flipper length, tarsus length and mass, little penguin bills grow slowly so bill metrics are good indicators of overall local food availability, quality and frequency of food delivered by parents during the protracted breeding season (Lack 1968, Gales 1987b, Wienecke *et al.* 2000). Previous studies indicate that bill morphology of little penguins is similar at three nearby colonies in south-eastern Australia (mean bill depth range: 12.24 - 12.49 mm females and 14.30 - 14.54 mm males, Gales 1988, Arnould *et al.* 2004). In contrast, significant differences exist between colonies in Western Australia, Tasmania and New Zealand (mean bill length: 39.6 vs 38.0 vs 35.2 - 37.9 mm respectively), which are separated by thousands of kilometres (reviewed by Klomp and Wooller 1988). Like many other penguins, little penguins exhibit male-biased SSD in bill size (reviewed by Agnew and Kerry 1995). SSD in bill size has not been recorded in little penguin chicks or fledglings that are on the point of leaving the colony for the first time (Renner and Davis 1999). Fledglings' bill sizes are 81 % (depth) and 91 % (length) of adults (Gales 1987b). SSD is therefore thought to develop after fledging.

I studied the morphology of the bills of little penguins to determine inter-sexual and inter-colony differences in their growth patterns. Based on similar bill morphology among three colonies within south-eastern Australia, I hypothesised that there would be no inter-colony variation in the bill morphology of adult little penguins, separated by 350 km, in South Australia. Because the bills of fledgling penguins are almost the same size as those of adults, I hypothesised that fledgling bills would reflect any adult bill size differences between colonies, and as with other studies, fledglings would exhibit no SSD in bill size. I examined a range of measures that have been used as indices of prey availability in little penguin populations, to determine whether they were related to any inter-colony differences in the rates of bill growth and eventual morphology. These included body masses of adults and fledglings, meal masses delivered by adults to the colony, maximum foraging ranges, maximum dive depths and foraging trip durations.

Methods

The study was conducted between 2004 and 2006 on two islands in South Australia: Troubridge Island (35°07´S, 137°50´E) in southern Gulf St Vincent, and Pearson Island (33°57´S, 134°15´E) off the west coast of Eyre Peninsula (Fig. 1 in Chapter 1). Morphometric bill measurements were made during the breeding season using digital callipers (± 0.01 mm). Bill depth (vertical bill thickness at the nares) (*BD*) and bill length (length of the exposed culmen) (*BL*) were recorded.

Two data sets of bill measurements from known-sex penguins were used as reference groups for the respective colonies (also used in Chapter 2). The sexes of the birds were determined by measuring the bills of pairs of penguins, which were attending their nest, with the larger bill indicating it was the male and the smaller bill the female (Gales 1988, Hocken and Russell 2002, Arnould *et al.* 2004). These birds were tagged with subcutaneously implanted glass-encapsulated TIRIS™ (Texas, USA) transponders, and were recorded at least five times with the same partner in the nest during the breeding season.

Kolmogorov-Smirnov tests were used to ensure all adult data sets for males and females were normally distributed and the Levene statistic tested for homogeneity of variance with an α level of 0.05. Results are reported in ranges and means ± 1 SE (mm). Ratios of *BD* to *BL* (a measure of bill robustness) were also compared between colonies and sexes.

Measurements of bills from chicks that were on the point of fledging, hereafter termed "fledglings" were made during the main breeding season (austral winter, June to August) of 2004 to 2006. All fledglings chosen for measurement had moulted > 70 % of their mesoptyle down (ensuring they were within days of fledging age, ~7-8 weeks) (Knight and Rogers 2004, Bool *et al.* 2007). Fledgling bill measurements were only included in the analyses if they were reared by parents that were provisioning two chicks until fledging age. Singleton fledglings were excluded because time since their sibling's death was unknown in each case and therefore provisioning rates may have changed dramatically at unknown stages of development. Singletons comprised 28 % to 39 % of the fledglings in any one breeding season at Troubridge Island and 37 % to 40 % at Pearson Island. Any growth bias that singleton fledglings exhibited over sibling fledglings used in this study was therefore likely to be similar between colonies. Fledglings from Troubridge and Pearson Islands were weighed (± 10 g) during the late afternoon, when their stomachs were empty, because parents only return from sea after dusk to feed them. Fledglings could not be sexed in the same way as the breeding pairs of adults and I did not have permits to take blood samples for DNA analyses to determine sex. I assumed that a bimodal distribution of fledgling bill measurements reflected inter-sexual differences.

Measures that describe food availability and foraging effort

Three metrics that reflect prey availability were obtained during the peak breeding season (winter); adult mass, meal mass returned ashore by parents, and meal mass fed to chicks. Adult mass was collected from breeding birds present (resting in active nests also containing chicks) in the colony during the day, when they had empty stomachs. Meal mass returned ashore was estimated from stomach contents collected using the stomach lavaging technique (Wilson 1984, Gales 1987a). Stomach content samples were taken from adults with chicks, but the chicks were not chicks used in other parts of this study. These samples were obtained shortly after dusk when adults returned from foraging trips. Adults were then re-fed with blended sardines and 10 % aqueous vitrate® before they were released (see Chapter 4 for methods). The adult stomach samples were drained on a 0.5 mm sieve and blotted dry with absorbent paper from below, before being weighed (± 0.01 g; samples also used for diet analyses in Chapter 4). Only samples greater than 1 % of the penguin body mass (minus the sample weight) were compared between colonies. The meal mass fed to chicks was determined for mid to large sized chicks (> 700 g), when demand for large meals was greatest. Meal mass was estimated by weighing individually-marked chicks two hours before and an hour after they were fed by their parents at dusk.

The maximum foraging ranges of adults during the breeding season was determined using satellite telemetry (Pearson Island 2004-2005, and Troubridge Island 2004-2006, see Chapter 6.). Satellite transmitters (30 g Cricket KiwiSat 202, Sirtrack, Havelock North, New Zealand) were attached to breeding penguins (in guard phase of breeding cycle), using Loctite® 401 glue, for one foraging trip, after which the devices were removed. Satellite location data were obtained through Service Argos Inc (Toulouse, France). The least accurate location classes (classified by Argos as *B* and *Z*) were discarded before the data was filtered for erroneous locations. The filter (McConnell *et al.* 1992) forced a maximum swim speed of 8.02 km.hr^{-1} using the R statistical software V.2.7.0 (R Development Core Team, R Foundation for Statistical Computing, Vienna) and the 'trip' package (version 1.1-5, M. Sumner, University of Tasmania, Hobart) (see methods in Chapter 6). The distance to the distal point of each foraging trip was calculated for 43 adults from Troubridge Island (n =24 in 2004, n =15 in 2005, n = 4 in 2006) and 17 from Pearson Island (n =10 in 2004, n = 7 in 2005). All trips were single foraging trips from different individuals (data also used for foraging behaviour analyses in Chapter 6).

The maximum dive depths attained during foraging trips were estimated using maximum depth recording tubes (Montague 1984), which were temporarily glued (open end backwards) to the backs of 18 breeding penguins (in guard phase of breeding cycle) from Troubridge Island and 14 from Pearson Island during winter 2005. The transparent, flexible plastic tubes were 90 mm x 1 mm in dimensions, sealed at one end and internally dusted with icing sugar. Water pressure encountered during the deepest dive forced water inside the tube, dissolving the sugar and so leaving a mark. Marks left by the dissolved sugar were calibrated to represent maximum water depth. The following depth equation was calculated from the marks left on each of five tubes attached at each 5 m increment of a 60 m weighted rope that was lowered and raised vertically into the ocean. Maximum depth (m) = $-19.921 \cdot ln\ (x) + 92.361$, where x is the length of sugar remaining in the tube (mm) ($r^2 = 0.99$, $n = 60$).

The duration of foraging trips were determined by data collected from an automatic TIRIS™ tag data logger (AMSKAN ltd., Victoria) during peak breeding season (winter). Small fences were placed to guide birds through a narrow gate where a radio frequency identification aerial was connected to the data logger to record the arrival and departure times of tagged penguins as they moved between the ocean and their burrows. All procedures were conducted under animal ethics approvals. Breeding success (chicks fledged per breeding pair) was also determined at both islands by monitoring the survival of chicks in marked nests.

Results

Inter-colony variation in adult bill morphology

Bill measurements were recorded from 114 breeding penguins (57 males and 57 females) tending eggs or chicks at Troubridge Island and 226 penguins (111 females and 115 males) at Pearson Island (data also used in Chapter 2; Table 1). *BD* and *BL* were strongly bimodal at both sites suggesting sexual dimorphism (Fig. 2). The bill measurements that were classified as male and female corresponded closely to each side of this bimodal distribution. The level of sexual bill dimorphism was similar at each colony. Male bill depths were on average 16.8 % larger than those of females at both Troubridge Island (15.31 ± 0.09 v 13.11 ± 0.08 mm) and Pearson Island (14.21 ± 0.5 v 12.17 ± 0.05 mm; Fig. 2). Male bill lengths were also on average larger than females by 4.2 % at Troubridge Island (39.94 ± 0.21 v 38.34 ± 0.19 mm) and 6.1 % at Pearson Island (39.30 ± 0.17 v 37.03 ± 0.14 mm). Within each sex, the bill depths of penguins from Troubridge Island were significantly larger than those at Pearson Island (7.7 % larger for males and females; $P < 0.001$ in both cases). Males had more robust bills (larger ratio of *BD*: *BL*) than females at both Troubridge Island (males 0.384 ± 0.003 vs females 0.342 ± 0.004) and Pearson Island (males 0.362 ± 0.002 vs females 0.329 ± 0.003). Between colonies, only the bills of males from Troubridge Island were significantly more robust than those from Pearson Island ($P < 0.001$).

Table 1. Mean bill depth (*BD*) and bill lengths (*BL*) (mm) for male and female little penguins from the Troubridge Island (females *n* = 57, males *n* = 57) and the Pearson Island samples (females *n* = 111, males *n* = 115).

		Troubridge Island			Pearson Island		
	Sex	Mean ± SE	Range	*P*	Mean ± SE	Range	*P*
BD	F	13.11 ± 0.08	11.6 – 14.3	<0.001	12.17 ± 0.05	11.13 – 13.68	<0.001
	M	15.31 ± 0.09	13.93 – 16.91		14.21 ± 0.5	12.92 – 15.71	
BL	F	38.34 ± 0.19	34.46 – 41.59	<0.001	37.03 ± 0.14	33.3 – 40.54	<0.001
	M	39.94 ± 0.21	36.72 – 43.31		39.30 ± 0.17	35.44 – 44.15	

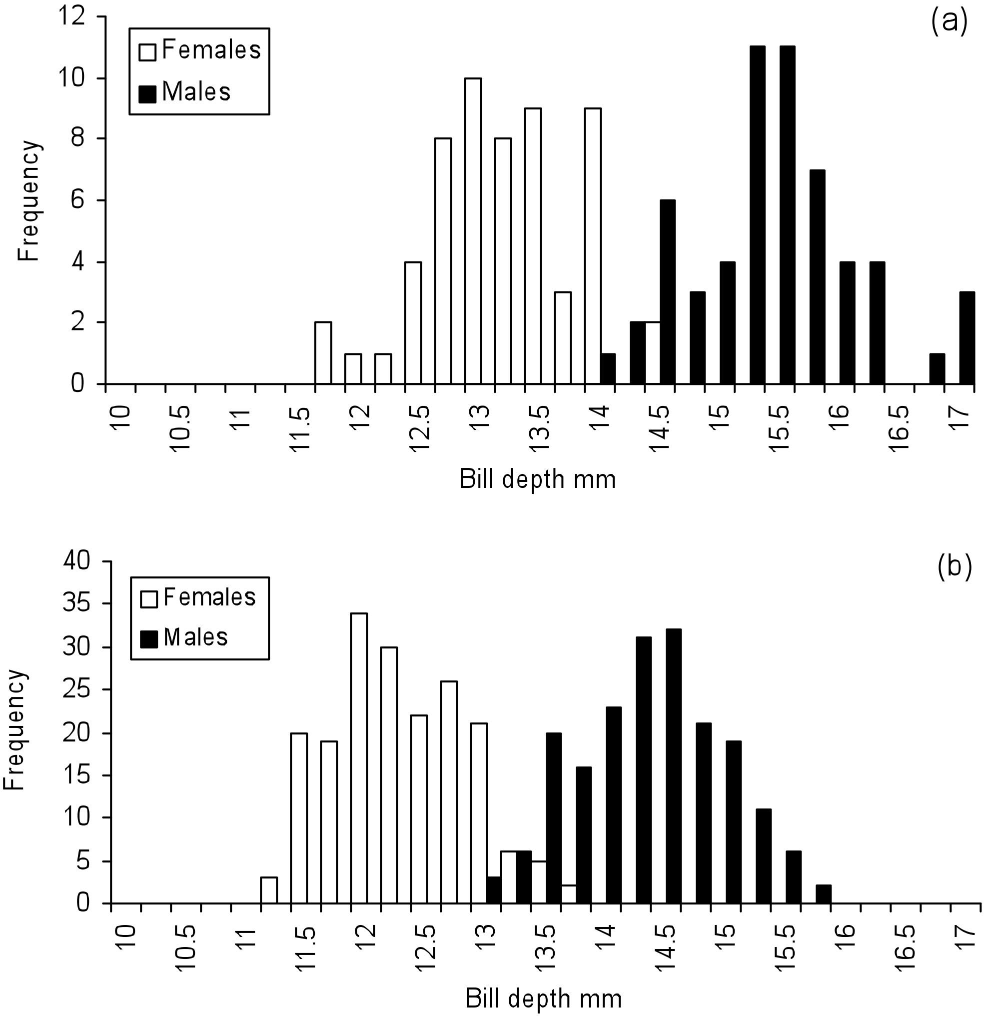

Figure 2. Frequency distribution of bill depth measurements for male (black) and female (white) little penguins from the Troubridge Island (a) and Pearson Island (b) in 0.25 mm size classes.

Inter-colony variation in fledgling morphology

The distribution of *BD* measurements from Troubridge Island fledglings was bimodal (Kolmogorov-Smirnov normality statistic = 0.160, $P = 0.002$, $n = 54$) whereas the distribution of Pearson Island fledgling *BD* measurements was uni-modal (Kolmogorov-Smirnov normality statistic = 0.068, $P = 0.200$, $n = 70$) (Fig. 3). Like the adults, fledglings from Troubridge Island had significantly larger *BD* measurements (mean 11.05 ± 0.09 v 10.45 ± 0.09 mm, Wilcoxon $W = 3530$, $Z = 4.256$, $P < 0.001$) and *BL* (mean 30.97 ± 0.33 v 29.60 ± 0.32 mm, Wilcoxon $W = 3724$, $Z = 3.278$, $P < 0.001$) than those for little penguins at Pearson Island. No significant differences existed between years for fledgling *BD* or *BL* at either colony ($P > 0.05$ in all cases).

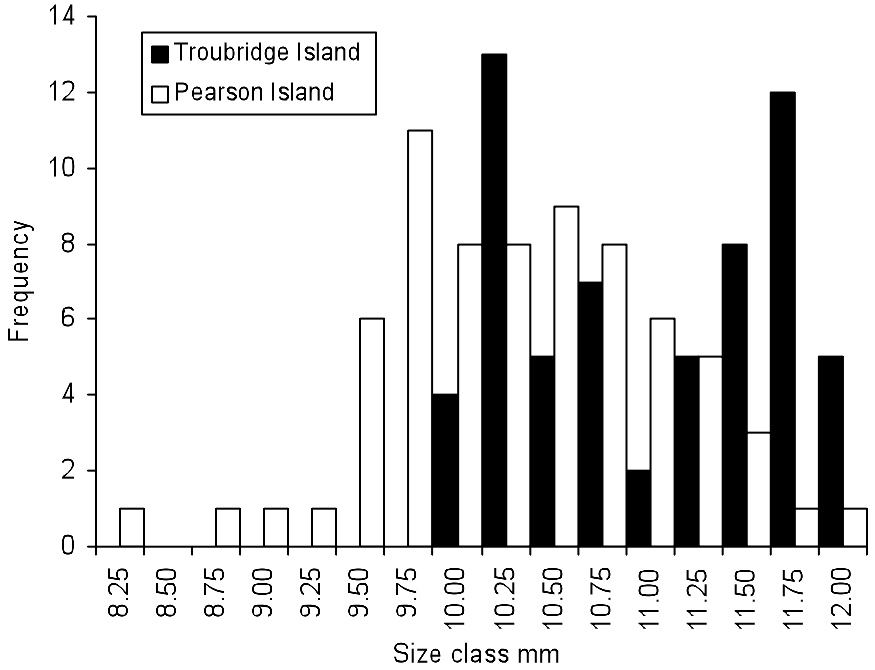

Figure 3. Frequency histogram of bill depths (mm) for fledgling little penguins from Pearson (white bars) and Troubridge (black bars) Islands, presented in 0.25 mm size class.

Inter-colony variation in body size, food and foraging variables, and breeding success

The body masses of fledglings and adults, the meals returned to the colony by adults, and the chick meals from Troubridge Island were all significantly larger than those from Pearson Island within each year and for all years pooled ($P < 0.05$ in all cases) (Table 2). Pearson Island adults had significantly greater maximum foraging ranges, maximum dive depths and longer foraging trips than those at Troubridge Island in all years (*P* <0.001 in all cases) (Table 2). The breeding success (chicks fledged per breeding pair) was greater at Troubridge Island than Pearson Island in all years Table 3.

Table 2. Summary table of mean fledging mass, adult mass, meal mass during winter (peak breeding), maximum foraging range, maximum dive depth and mean length of fishing trips during the breeding season at Troubridge and Pearson Islands.

	Troubridge Island		Pearson Island		
	Mean ± SE	*n* (years)	Mean ± SE	*n* (years)	*P*
Mean mass at fledgling mass (g)	1236.7±14.4	108 (2004-06)	1005.6±14.2	117 (2004-06)	<0.001
Mean meal mass delivered to individual chicks (g)	182.5±14.2	56 (2005-06)	152.8±14.1	53 (2005-06)	<0.001
Mean mass of adult s (g)	1300±7.6	432 (2004-06)	1071±6.6	447 (2004-06)	<0.001
Mean meal mass brought ashore by adults (g)	140.2±9.9	101 (2004-06)	122.3±12.3	43 (2004-05)	<0.001
Mean maximum distance of foraging trips of breeding adults (km)	12.81±0.6	43 (2004-06)	41.71±7.4	27 (2004-05)	<0.001
Mean maximum dive depth (m)	25.14±1.9	18 (2005)	42.5±1.2	14 (2005)	<0.01
Mean duration of fishing trips (d) (using mean durations of trips by individuals)	2.09±0.15	129 (2004-05)	2.5±0.15	327 (2004-05)	0.048

Table 3. Breeding success of little penguins at Troubridge Island (2004-2006) and Pearson Island (2004-2005).

	Troubridge Island		Pearson Island	
Year	Chicks fledged per pair	*n* (nests)	Chicks fledged per pair	*n* (nests)
2004	1.11	42	0.56	134
2005	0.91	122	0.62	58
2006	0.85	67		

Discussion

Variation in the bill morphology of adult little penguins exists across their range (Kinsky and Falla 1976, Klomp and Wooller 1988, Wienecke *et al.* 2000, Miyazaki and Waas 2003, Arnould *et al.* 2004, Overeem *et al.* 2006), but variation across the central part of their range in southern Australia, has not previously been reported. In this study, the variation in bill morphology between colonies just 350 km apart, is considerably greater than the variation between nearby colonies in south-eastern Australia (7.7 % vs 1-2 % variation in *BD*) (Arnould *et al.* 2004) and New Zealand (Kinsky and Falla 1976, Gales 1988, Meredith and Sin 1988, Renner and Davis 1999). The differences in adult bill size between Troubridge and Pearson Islands were also reflected in the bill sizes of the fledglings, which indicate that these morphological differences between colonies were not age-specific.

The colony variation in morphology across age groups may reflect genetic differences (Price and Grant 1984) and/or, as suggested by this study, geographic differences in food, foraging success and energy requirements to obtain and metabolise food (Cooch *et al.* 1991). Results from this study indicate that the two islands differed in the rates of provisioning and where the penguins could fish, which accounted for the variation in morphology between colonies. One can infer that food availability was greater around Troubridge Island over the three consecutive years of this study, providing better nutrition for the growth of chicks. Penguins at Troubridge Island were able to forage closer to the colony, return more frequently to feed their chicks and catch prey within shallower maximum dive depths. Several other studies suggest that changes in prey availability affect growth rates of geese, blackbirds and red-billed tropic birds *Phaethon aetherus*, before and after they fledge (James 1983, Cooch *et al.* 1991, Castillo-Guerrero *et al.* 2011). James (1983) found that adult blackbirds from two regions varied in size, but chicks that were swapped between the regions grew to resemble their foster parents rather than their biological ones. A chick-swapping experiment on chinstrap penguins *Pygoscelis antarctica* also showed that chick growth variation was seasonal rather than a result of parental quality (Moreno *et al.* 1997). Reduced food availability and lower provisioning rates also affected little penguin growth rates (including bills and other variables) at Penguin Island (Wienecke *et al.* 2000) and Phillip Island, Victoria (Chiaradia and Nisbet 2006). Similarly, my study supports these findings that better nutrition results in fledglings with larger bills and larger masses. Given continued optimal food availability, larger fledglings are more likely to grow into larger adults (James 1983).

The inter-colony differences in bill morphology across age groups suggest that juveniles do not intermix between colonies and that they return to their natal colony to breed. Such natal philopatry can result in population subdivision, which would be consistent with genetic differences that exist between some colonies of little penguins (Overeem *et al.* 2007). Indeed, studies in Victoria indicate that young penguins return to their natal colony to breed (Reilly and Cullen 1983) increasing population subdivision.

The level of sexual bill dimorphism observed between the sexes in this study is greater than has been observed in other penguins (Minguez *et al.* 2001), but is similar to what has been observed in other little penguin populations (Hocken and Russell, 2002, Arnould *et al.* 2004). The evolution of SSD in birds, particularly in bill morphology, may be a result of selective character displacement to reduce inter-sexual competition for food, and/or female mate-choice for larger males, where male size influences breeding success through defensive behaviour (Moody *et al.* 2005). Selective character displacement to reduce inter-sexual competition appears plausible for little penguins at Phillip Island where males and females have evolved to target different prey and prey of different sizes (Shaw *et al.* 2007), or forage in different locations (Collins *et al.* 1999). Equally, female mate-choice could improve little penguin reproductive success because, in one study, male head size was positively correlated with breeding success, where large males were more adept at protecting the nest and they nested at elevations (preferred sites) used by other large males (Miyazaki and Waas 2003). In contrast, female size appears unrelated to reproductive success (Waas 1988, Waas 1991, Miyazaki and Waas 2003). If inter-sexual competition for food were a driver of SSD, we would expect SSD to have evolved to a greater extent at colonies where food was consistently more limiting, such as Pearson Island. Instead, my data showed that the relative difference in SSD between sexes at both colonies was equal, irrespective of food availability. Further dietary work on penguins from these colonies (Chapter 4) indicates that there are no difference in male and female diets which does not support the possibility that bill differences are related to niche separation (of diet). As such, female mate-choice (of males with large bills) may be a stronger contributing factor for SSD. Alternatively there may be selection for females to be a little smaller relative to the males because of the increased energetic costs of laying eggs.

SSD in bill size can develop at different growth phases in different species. Cory's shearwaters *Calonectris diomedea* (Bretagnolle and Thibault 1995) and Magellanic penguins *Spheniscus magellanicus* (Scolaro 1987) exhibit SSD in bills before fledging age, compared with previous little penguin studies that have found no bill size dimorphism in fledging chicks (Renner and Davis 1999). In contrast, this study showed that little penguin fledglings from Troubridge Island exhibited bimodal BD distributions, but those from Pearson Island did not. Given that BD was the most dimorphic variable between the sexes of adults, the bimodal BD distribution of these fledglings at Troubridge Island also suggests male-biased sexual dimorphism in chick bill size. This apparent sexual size dimorphism in the Troubridge Island chicks may either indicate a difference in the ability of male and female siblings in obtaining food from their parents (Clutton-Brock 1991, Müller *et al.* 2005), intersexual differences in metabolic rates (Krijgsveld *et al.* 1998) and/or parents allocating food differently based on the sex of offspring (Magrath *et al.* 2007).

The lack of SSD in the Pearson Island fledglings indicates that males and females were equally provisioned, or if they were not, their differences in metabolic rates resulted in equal bill growth. We cannot discern between these causes, but it is worth speculating how they affect SSD in adult little penguins at different sites. Firstly, at Pearson Island SSD may be an artefact of different survival rates of juveniles, specifically greater survival of the largest males and the smallest females. Alternatively, at Pearson Island, SSD may develop after fledging, presumably within the four weeks it takes for a newly fledged juvenile to grow its bill to adult size, as estimated by Gales (1987b). In contrast, at Troubridge Island where chicks were better provisioned (inferred from higher breeding success), SSD appears to develop before fledging. Similarly, Chiaradia and Nisbet (2006) found delayed growth responses in little penguin chicks (body mass) in years of poor breeding where provisioning rates were reduced.

If male fledglings at Troubridge Island reached (phenotypic) maturity at an earlier age, which may be suggested by early development of SSD, then we may be able to investigate whether growing a large bill early in life influences the onset of breeding or lifetime reproductive success. We may also expect the larger size of the chicks at Troubridge (assuming that body mass reflects the amount of body fat) to be reflected in increased survival as well, as is the case for crested terns *Thalasseus bergii* (McLeay *et al.* 2009) and little penguins at Phillip Island (Dann 1987). Chick growth can also reflect breeding later in life, which has been reported for common tern *Sterna hirundo* chicks where those chicks with high mass at fledging bred earlier and more successfully (Becker *et al.* 2001).

The difference in the extent of SSD in fledglings between colonies suggests that male bills do not intrinsically grow faster than females before fledging, because male bills only grow faster when food resources are good. Other possibilities are that parental provisioning is greater for male chicks than female chicks through competition (Müller et al. 2005) or parental preference (Schauroth and Becker 2008) when food is abundant. However, if differential parental provisioning were the case, we may expect an unbiased sex ratio among fledglings (with more males), which did not appear to be the case (at least at Troubridge Island). Further testing could investigate whether it is provisioning of food that determines SSD in fledglings (at some colonies) through cross-fostering experiments where chicks of different sexes are translocated between colonies.

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Chapter 4: The diets of little penguins *Eudyptula minor* and their reliance on Australian anchovy *Engraulis australis* in South Australia.

Abstract

Little penguins *Eudyptula minor* are important consumers of small pelagic fish in coastal pelagic ecosystem in southern Australia. Knowledge of the variation in little penguin diets provides an understanding of their role in marine ecosystems and their sensitivity to changes in available prey. The diets of little penguins from eight colonies in the eastern Great Australian Bight (GAB) were sampled over three years to assess the spatial and temporal variation in prey composition and biomass. This study also investigated whether environmental and biological factors were linked to differences in these diets and whether key prey species abundance influenced the onset of breeding. The most frequently consumed prey species (in 92 % of samples) at seven colonies was Australian anchovy (*Engraulis australis*), which accounted for 67 % of their estimated prey biomass. The universally high proportion of anchovy resulted in low dietary variation among little penguin colonies contrasting the more diverse diets reported for other regions across the species range. However, in common with other regions, prey were generally 50 - 90 mm in length and 2 - 6 g in mass with the exception of the much larger southern sea garfish (*Hyporhamphus melanochir*) (199 mm, 23 g), being the second most important prey species. Although juvenile sardine *Sardinops sagax* are also abundant in the eastern GAB, penguins appear to preferentially target anchovy, which are more energy dense and may be easier to catch. Whole meal masses and anchovy mass (within meals) peaked during winter and summer months, coinciding with the breeding and moulting period, respectively. Anchovy biomasses in the diets were also positively correlated with the number of nests containing eggs at the time of sampling, suggesting that breeding is timed to coincide with high anchovy availability. The reliability of anchovy availability year-round in South Australia may account for the prolonged and asynchronous breeding seasons, as well as the opportunity for double brooding in little penguins.

Key words: little penguin, *Eudyptula minor*, diet, Australian anchovy, *Engraulis australis*

Introduction

Seabirds are well adapted to respond to unpredictable spatial and temporal fluctuations in the availability of their prey (Burger and Piatt 1990). Seabirds have prolonged life cycles, wide ranging foraging strategies and some have an ability to store fat reserves. They also readily abandon offspring during periods of limited food while they can quickly revert to breeding again under better conditions (Lack 1968). Despite these traits, anthropogenic impacts on food webs (such as competition with fisheries) have resulted in the declines of many seabird populations, particularly those that rely on a single prominent prey species (Crawford and Shelton 1978, Blake 1984, Monaghan *et al.* 1989, Tasker *et al.* 2000, Wanless *et al.* 2005). An understanding of the natural variation in seabird diets enables ecologists to determine how adaptable seabirds are to changes in available food resources, particularly dominant prey species that are also targeted by fisheries.

Changes in seabird diets often reflect the relative abundances of local prey (Moore *et al.* 1999, Chiaradia *et al.* 2010), but the strength of these relationships is dependent on whether the seabird is a generalist or a selective forager (Monaghan *et al.* 1992, Dann *et al.* 2000). Diets of selective foragers reflect the abundance of their key prey more closely, whereas generalists will switch and mix prey depending on what is most available (Hilton *et al.* 2000). Penguins that live in mid-latitude coastal habitats, such as little penguins *Eudyptula minor*, tend to have more diverse diets (Gales and Pemberton 1990) than penguin species in higher latitudes where pelagic environments are more homogeneous (Brown and Klages 1987, Williams *et al.* 1992, Moore *et al.* 1999, Lynnes *et al.* 2004). Across their Australasian distribution, little penguins are known to be generalist predators typically feeding within 20 km of their colonies on a diverse range of locally abundant small fish and cephalopod species (Gales and Pemberton 1990, Cullen *et al.* 1992, Collins *et al.* 1999, Chiaradia *et al.* 2003).

At little penguin colonies in Australia the single most common prey species typically comprises between 26 and 61 % of all prey items, not necessarily the same prey at each location (Klomp and Wooller 1988, Montague and Cullen 1988, Gales and Pemberton 1990). There is a greater range in these values for subantarctic penguins

(33 - 86 % food items, Olsson and North 1997, Hull 1999, Clausen et al. 2005) and these values are higher in Antarctic penguins (up to 99.9 % by mass, Lynnes et al. 2004). The ability and opportunity for little penguins to catch and consume a diverse suite of prey species will reduce their reliance on the availability of a single prey species. By targeting multiple prey species, penguin populations may be buffered against marked changes in the availability of one or more prey taxa. However, targeting multiple prey species may also present challenges including the need for adaptive foraging strategies, and also adaptive digestive abilities for mixing and switching prey (Hilton *et al.* 2000).

Sardine *Sardinops sagax* and Australian anchovy *Engraulis australis* are commonly reported in little penguin diets in Australia (Stahel and Gales 1987, Klomp and Wooller 1988, Gales and Pemberton 1990, Cullen *et al.* 1992). These two fish were once the main prey of little penguins from colonies in south-eastern Australia (i.e. Phillip Island). However, sardines (and to a lesser degree anchovies) decreased in the diets of little penguin foraging in Victoria waters after commercial sardine fishing increased in the early 1990s (Niera *et al.* 1999) and after two events of sardine mass mortality in 1995 and 1998 (Chiaradia *et al.* 2003, Chiaradia *et al.* 2010). The diets of little penguins in South Australia have not been studied, but sardines and anchovies are also abundant in the region where they spawn year-round although peak during summer and early autumn (Ward *et al.* 2001a, Ward *et al.* 2001b, Dimmlich *et al.* 2004, Ward *et al.* 2006). Within 4 - 12 months, the juvenile fish are 50 – 100 mm in length (Ward *et al.* 2005, Dimmlich and Ward 2006), which is the prey size preferred by little penguins (Klomp and Wooller 1988, Gales and Pemberton 1990, Cullen *et al.* 1992).

Changes in local prey availability can influence the onset of seabird breeding seasons, as well as egg laying synchrony within a colony (van Heezik and Davis 1990, Cullen *et al.* 1992, Monaghan *et al.* 1992, Chiaradia *et al.* 2002). Across the range of little penguins, the onset and duration of breeding seasons differs markedly, most likely, in response to variation in prey availability. Most penguin colonies in New Zealand and south-eastern Australia breed between September and February (Goldsworthy *et al.* 2000, Chiaradia *et al.* 2003, Miyazaki and Waas 2003, Weerheim *et al.* 2003), whereas colonies in South and Western Australia breed earlier, from April until November, often with two peak-laying periods (double or repeat brooding) in South Australia (Klomp and Wooller 1988, Johnson and Wiebkin 2008). Similarly, prolonged and variable breeding seasons exist between colonies of other low latitude penguins such as African penguins *Spheniscus demersus* and Galapagos penguins *S. mendiculus*. In these species, variable breeding seasons tend to correlate with variable diets (Heath and Randall 1985) and not with the abundance of a single prey species.

This study aimed to describe the diets of little penguins in South Australia. Diets from eight colonies were described and compared using composition, prey size, nutritional value and meal masses, across years and seasons. I also investigated whether dietary variation was linked to biological characteristics such as body mass, sex and bill size, or to ecological characteristics such as the onset of breeding, or to environmental conditions such as sea-surface temperature. I hypothesised that the diet of little penguins in South Australia would be as diverse as those from other regions, and as generalist predators, would consume the most locally abundant small pelagic fish species (anchovy and sardine), the temporal abundance of which would influence the timing of breeding.

Methods

Study sites

The study was conducted on the following islands in South Australia: Troubridge Island (35°07'S, 137°50'E), Reevesby Island (34°32'S, 136°17'E), Greenly Island (34°39'S, 134°46'E), Pearson Island (33°57'S, 134°15'E), Olive Island (32°43'S, 133°58'E), West Franklin Island (32°27'S, 133°39'E), West Island (35°37'S, 138°36'E) and Granite Island (35°33'S, 138°37'E) (Fig. 1 in Chapter 1). Troubridge and Reevesby Islands are located in shallow gulfs (< 40 m deep), which are less exposed to prevailing weather than the open continental shelf (< 100 m deep) where Greenly, Pearson, Olive and West Franklin Islands are located. West and Granite Islands are also located on the shelf (3 km apart) where a large bay provides protection from westerly weather. Austral seasons are referred to in this chapter (autumn is March - May, winter is June - August, spring is September - November and summer is December - February).

Sample collection

Samples of stomach contents were collected between September 2003 and October 2006. Sampling effort was increased during the winter breeding months, and reduced in summer (Table 1). Adult little penguins weighing more than 900g were captured shortly after dusk as they arrived on shore from a foraging trip. Birds were weighed using a spring balance (± 5 g). Bill depth (vertical bill thickness at the nares) (*BD*) and bill length (length of the exposed culmen) (*BL*) were recorded (± 0.01 mm), using digital callipers for the purpose of allocating sex using discriminant functions (Chapter 2). In all but one field trip, samples were collected on a single night. Daily variation in diet was investigated by collecting 65 samples over 7 consecutive days at Troubridge Island in July 2004.

Stomach content samples were collected using the stomach lavaging technique (Wilson 1984, Gales 1987) where freshwater was pumped into the stomach through a 4 mm diameter duodenal tube, Unomedical™. The lavaging process was repeated up to four times, or less if regurgitated water was clear or green, the latter of which indicated the presence of bile (Horne *et al.* 1985). If water did not run clear within four lavages, the sample was not complete and it was not used for meal biomass analyses. After lavaging, penguins were fed with 40 ml 10 % aqueous Vy-Trate ® and 50 g of blended (beheaded and scaled) sardine through a 6 mm diameter feeding tube, Unomedical™ (see methods in Chiaradia *et al.* 2003). Birds were placed in a quiet, dark soft-mesh pen for 10 - 20 min for observation to ensure they were fit before being released at the location of capture. No penguin was subjected to repeat lavage-sampling procedure. Birds from regularly visited colonies were implanted with 23 mm TIRIS™ Radio Frequency Identification (RFID) transponder tags (Texas, USA) to ensure that recaptured individuals could be recognised. Animal Ethics approval was granted for all procedures.

Table 1. The number of little penguins from which diet samples were collected from each colony (*n*) on multiple occasions, the number of samples used in the biomass analyses (in parentheses) and the mean sample wet weights (g ± S.E.). -, not sampled. Samples were also taken on one occasion at Greenly in November 2003 (n= 27, 19 used in biomass analyses, mean sample weight = 58 ± 18 g), at Olive Island in July 2006 (n= 10, 7 used in biomass analyses, mean sample weight = 99 ± 29 g), and at Franklin Island in December 2003 (*n*= 27, 22 used in biomass analyses, mean sample weight = 148 ± 19 g).

		Granite			Pearson			Reevesby			Troubridge			West		
Year	Month	*n*		sample wt	*n*		sample wt	*n*		sample wt	*n*		sample wt	*n*		sample wt
2003	Sept			-	41	(5)	287 ± 28			-			-			-
	Oct			-			-			-	33	(19)	78 ± 14			-
	Nov			-			-	30	(24)	120 ± 16			-			-
	Dec			-	36	(34)	132 ± 13			-			-			-
2004	April			-			-	35	(5)	60 ± 43			-			-
	May			-	36	(18)	122 ± 19			-	43	(29)	181 ± 22			-
	June			-			-	32	(26)	210 ± 14			-			-
	July			-	40	(31)	113 ±15			-	65	(50)	144 ± 15			-
	Aug			-			-	34	(6)	160 ± 31	19	(17)	137 ± 25			-
	Sep			-			-			-			-			-
	Nov			-	41	(33)	127 ± 13			-			-			-
2005	Mar			-			-			-	26	(14)	54 ±13			-
	Apr			-			-	6	(3)	40 ± 16			-			-
	May			-			-			-	12	(14)	117 ± 19			-
	June			-			-			-			-			-
	July			-	15	(12)	146 ± 21			-			-			-
	Aug			-			-			-	16	(11)	191 ± 34			-
	Sept			-			-	19	(14)	173 ± 23	12	(11)	167 ± 27			-
	Oct			-			-			-	10	(10)	146 ± 43			-
	Nov			-			-			-	11	(11)	178 ± 34			-
2006	April			-			-			-	10	(4)	34 ± 17			-
	May			-			-			-	10	(6)	58 ± 14			-
	June			-			-			-	5	(3)	75 ± 34			-
	July	1	(1)	44			-			-						-
	Aug	6	(5)	79 ± 17			-			-	8	7	114 ± 15			-
	Sept	6	(6)	31 ± 5			-			-	8	5	75 ± 23	4	(4)	58 ± 23
	Oct	6	(4)	54 ± 9			-			-			-	3	(3)	51 ± 22

Sample processing

Stomach samples were frozen or preserved in 70 % ethanol until they were processed in the laboratory. Samples were drained on a 0.25 mm sieve and blotted from underneath, then weighed as a wet weight (± 0.01 g). They were ranked (1 - 4) based on their level of digestion. Level 1 contained at least one whole fish or squid; level 2 contained at least one fish head, tail or squid mantle; level 3 contained bones and/or otoliths; 4 was very digested and homogenised, grey in colour, granular with no bones, however beaks and eroded otoliths were sometimes present. Samples were sieved using 0.5 and 0.25 mm sieves stacked above one another and flushed with water, in order to sort otoliths, cephalopod beaks and identifiable parts. I assumed that the retrieved prey items (other than eroded squid beaks) were those ingested the same day (Gales 1988). Whole prey items were counted, weighed and measured. Otoliths, shells and plastic fragments were stored dry and all other items were stored in 70 % ethanol. One person (AW) identified fish otoliths and cephalopod beaks using reference manuals and collections at SARDI Aquatic Sciences (S.D. Goldsworthy and B. Page unpublished data, Cullen *et al.* 1992, Lu and Ickeringill 2002, Ye *et al.* 2002, Furlani *et al.* 2007). The greatest number of left or right otoliths and upper or lower beaks for each prey species, together with the number of paired otoliths and beaks as well as other prey remains, determined the minimum number of items consumed. Numerical abundance of larval fish and crabs was estimated in relative measures of abundance (1, 10, 100) because they were often fragmented.

Whole prey were weighed and biomasses of prey that were represented as partial items were estimated from otolith or beak length-body mass regressions (Cullen *et al.* 1992, Furlani *et al.* 2007, this paper). Cephalopod beaks are known to persist and accumulate in seabird stomachs for many days (Furness *et al.* 1984). To reduce over-estimation of cephalopods, only beaks that were either removed from the buccal mass or those that were free with no evidence of erosion were used for biomass estimates (Hull 1999). Because slightly more left otoliths were recovered, the lengths of all identifiable left sagittal otoliths, and the hoods of lower squid beaks were measured (± 0.00001 mm) using a stereo dissecting microscope (7 x magnification), an eye-piece mounted video camera and the Image-Pro Plus ™

(Media Cybernetics, Inc) image analysis program. To account for variation in otolith condition and size reduction resulting from stomach digestion (Caines 2005), otoliths were categorised into condition classes as follows: Class 1, undigested condition; Class 2, lacked surface sheen, appeared opaque, eroded proximal edges, sulcus edges were no longer sharply defined, edge features such as crenulations and spines remained present, albeit reduced in size and rounded; Class 3, identifiable but lacking edge features, rostra rounded, surfaces pitted and general appearance very eroded. Size correction factors were calculated for Classes 2 and 3 to determine the percentage by which they had been eroded. To do this, all otoliths of each species were divided into size categories (small, medium and large: delineated retrospectively by increments of 33.3 % of the size range of all otoliths found in all samples pooled for the respective species). The difference in the species-specific mean otolith sizes between Classes 1 and 2, and Classes 1 and 3 within each size category were used for the development of these correction factors. These were then used to calculate the original size of each eroded otolith in Classes 2 and 3 (Table 2.).

Estimated meal biomass (EMB) prior to digestion was determined from otolith and beak regressions as well as whole prey and estimated weights of larval fish and crab megalopa larvae. Larval fish otoliths were too small for extraction and identification and so prey biomass, along with crab larvae were estimated by proportion of the wet mass. EMB was then standardised by proportion of the penguin's net body mass (penguin body mass minus the stomach content wet mass) to ensure variation in penguin stomach size did not bias analyses. The age of prey items was also estimated for four species, where age : otolith size regressions were available.

Table 2. The numbers of left otoliths and lower beaks measured in each erosion class, the mean otolith and lower beak hood lengths ± S.E., and percentage decrease in otolith length (from original size) due to erosion.

	n				Mean length ± SE mm of medium size class			Percentage decrease from original size	
Species	Class 1	Class 2	Class 3	total	Class 1	Class 2	Class 3	Class 2	Class 3
Engraulis australis	2202	1765	3832	7799	2.34±0.01	2.19±0.01	1.91±0.01	7	18
Sardinops sagax	1076	497	356	1929	1.49±0.01	1.31±0.01	1.28±0.01	2.7	14
Spratelloides robustus	485	131	33	649	1.32±0.01	1.22±0.01	1.15±0.03	7	13
Parapriacanthus elongatus	316	141	182	639	3.00±0.03	2.78±0.05	2.52±0.04	7.1	18.3
Arripis georgiana	190	96	306	592	2.66±0.02	2.47±0.02	2.10±0.02	6.7	21
Emmelichthys nitidus	302	83	192	577	1.82±0.02	1.77±0.05	1.67±0.03	2.4	8.1
Atherinason hepsetoides	273	109	169	551	2.86±0.02	2.71±0.02	2.40±0.03	5	16
Hyporhamphus melanochir	158	39	167	364	3.96±0.07	3.79±0.14	3.06±0.08	4	23
Scomberesox saurus	52	6	3	61	1.27±0.03	1.34±0.11	0.91±0.05		29
Acanthaluteres spilomelanurus	27	2	2	31	0.87±0.03	0.52±0.00	0.55±0.02	39	36
Parequula melbournensis	15	3	10	28	4.28±0.15	3.54±0.29	3.30±0.16	17	23
Trachurus declivus	6			6	4.61±0.08				
Scorpis lineolata			2	2			3.34±0.06		
Scomber australasicus	4			4	2.18±0.14				
Aldrichetta forsteri			1	1			1.40		
Sp 1	147	41	91	279	1.05±0.02	0.97±0.02	1.09±0.02	8	-3
Unknown (inc Sp 1)				422					
Nototodarus gouldi	103	489		592	2.34±0.03				

Analyses of measures

Samples with an EMB greater than 1% of the penguin's net body mass (penguin weight minus the sample wet weight) were used for diet analyses. Results are reported in ranges and means ± 1 S.E. (mm). Diets were described following three indices from Chiaradia *et al.* (2003):

- percent frequency of occurrence (FO) (the proportion of samples collected that contained each taxa),
- percent numerical abundance (NA) (the minimum number of individuals of a taxa as a proportion of all individuals within a stomach sample) and
- percent estimated relative abundance (ERB) (the proportional biomass of each species within a stomach sample).

Taxa that were not considered to be prey such as shells, nematodes, isopods and remnants of plastic were excluded from NA and ERB.

A niche overlap index (modified from Schoener 1968) was used to determine the percent similarity or overlap in diet composition and proportion between colonies. The equation follows as:

$$O = 1 - 0.5 \times \sum_{j=1}^{n} |p_{1j} - p_{2j}|$$

where p_{1j} and p_{2j} are the percent biomass or the percent numerical abundance of the *j*th prey taxon for each of two colonies The overlap (*O*) equals 1 if the two colonies consumed equal quantities of the same prey and equals 0 if both colonies consumed completely different prey.

Multivariate regression tree (MRT) analysis ('mvpart' Package, V 1.2-4, G. De'ath, Australian Institute of Marine Science, Townville) was used in R statistical software V.2.7.0 (R Development Core Team (2009), R Foundation for Statistical Computing, Vienna) to investigate how prey species composition and biomass within individual diets correlated with temporal, environmental and biological variables (De'ath 2003, Sheaves 2006). Variables included season, year, sea-surface temperature (SST) (monthly mean temperature ± 0.1 °C with in 20 km radius around each colony, http://poet.jpl.nasa.gov), breeding indices (proportion of monitored active burrows in the colony containing eggs, chicks, or either eggs or chicks at the time of sampling diets), penguin sex, bill depth (*BD*), bill length (*BL*), and net penguin weight. MRT sequentially splits the data, each based on a simple rule that is chosen to minimise variability of samples within clusters. Models were performed 500 times and the best tree was that with the lowest cross validation error (CV error) within 1 SE, which is the prediction error for the tree size that minimises variability (Sheaves 2006).

Other correlations

Correlations between the actual biomass of key prey species and environmental and ecological variables were also investigated. These included midday sea swell height (sourced from www.buoyweather.com), SST (monthly mean temperature °C within a 20 km radius around each colony), breeding indices, body mass and body condition index (mass/*BD*). Relationships between prey otolith lengths of key prey (as a proxy for fish size) and penguin bill size (*BD* and *BL*) were investigated to determine if bill size was correlated with prey size.

All data was checked for assumptions of normality and homoscedasticity using Komolgorov-Smirnov test and Levene's test prior to choosing parametric or non-parametric tests and correlations (Pearson's or Spearman's, respectively). Average values are presented ± S.E.

Nutritional value of prey

In order to quantify nutritional status (protein, lipid and other organic matter) of prey, 111 fish from 14 prey species were harvested from local waters (Gulf St Vincent, Spencer Gulf and eastern Great Australian Bight) during 2004 and 2005. Fish were oven-dried (45 °C) until consecutive daily dry weights stabilised (~8 - 10 d) before they were ground with a mortar and pestle, then weighed (± 0.0001 g). Where individual fish were too small for nutritional analyses (0.5 - 6 g), they were combined to form larger samples. Lipid and wax ester concentrations were extracted with diethyl ether petroleum from duplicate samples (0.6 - 6.7 g) placed in soxhlet thimbles (40 x 12 mm), sealed with cotton wool. Samples were further dried at 45 °C overnight before they were again weighed to calculate the amount of lipid that had been extracted.

The semi-micro Kjeldahl technique was used to calculate nitrogen concentrations in duplicate samples (0.2500 ± 0.100 g). Each sample was weighed, encased in a vessel of folded qualitative filter paper and placed in a glass digestion tube (250 x 20 mm) with a Kjeldtab catalyst tablet of 3.5 g K_2SO_4 and 3.5 mg Se (Foss Tecator, Sweden cat no 1527-0003) and 6 ml AR concentrated HCl. A Tecator 2012 Digestor digested samples at 250° C for 10 min and then 420° C for 1 h. Upon cooling, the samples were steam-distilled and titrated (0.025 M HCl) in a Vapodest 5 analyser (Gerhardt, Bonn, Germany) to determine nitrogen content. Blank controls included filter paper alone, empty tubes and $(NH_4)_2SO_4$. Protein was estimated as % N x 6.25.

Ash concentrations were determined from lipid-free samples burned in a kiln for 12 h. Protein concentrations were subtracted from the remaining organic ash weights to obtain remaining organic matter (chitin and other carbohydrate). Gross dry weight energetic values were calculated according to Ricklefs (1974) where lipid = 39.5 $kJ.g^{-1}$, protein = 18.0 $kJ.g^{-1}$and carbohydrate and chitin = 17.2 $kJ.g^{-1}$.

Results

Stomach samples from 743 penguins were obtained, of which 493 (66 %) were used in the dietary analyses. Of these, 269 (55 %) were from males, 220 (45 %) were from females and 4 (0.8 %) were from birds of unknown sex. The mean of estimated daily meal biomasses (EMB) was 147 ± 5 g (max 497 g) and 13 ± 0.5 % of net body mass (max 50 %). The mean of wet meal masses was 132 ± 4 g (max 432 g) and 11 ± 0.4 % (max 38 %) of net body mass. Daily meal masses were skewed towards low masses, however a small second mode was evident between 250 - 275 g (estimated at 21 - 23 % of mean net body mass of 1191 g; Fig. 2). EMB as a proportion of net body mass was not significantly different between colonies, years or between sexes within colonies ($P > 0.05$) but they differed between seasons ($P < 0.001$). The largest daily meals were in winter (16 % of net body mass) and early summer (19 %) whereas the smallest daily meals were in spring (11 %) and autumn (10 %). Diets from the eight colonies comprised of 23 fish species, four of which were unidentified, as well as one squid species, one unidentified crab species (larval megalopa stage), one prawn species and unidentified larval fish (Table 3). Additional items included shells, cuttlefish bones, isopods, nematodes and hard plastic, which were not considered to be prey items. Most samples were ranked as digestion level 2 (40 %), followed by level 3 (25 %), level 4 (20 %) and level 1 (15 %).

Figure 2. Frequency distributions of estimated meal biomasses (before digestion) in size categories of 25 g (bars), and the estimated energy consumed for each daily meal size (line), based on an average diet energy density of 5.46 kJ/g (this paper).

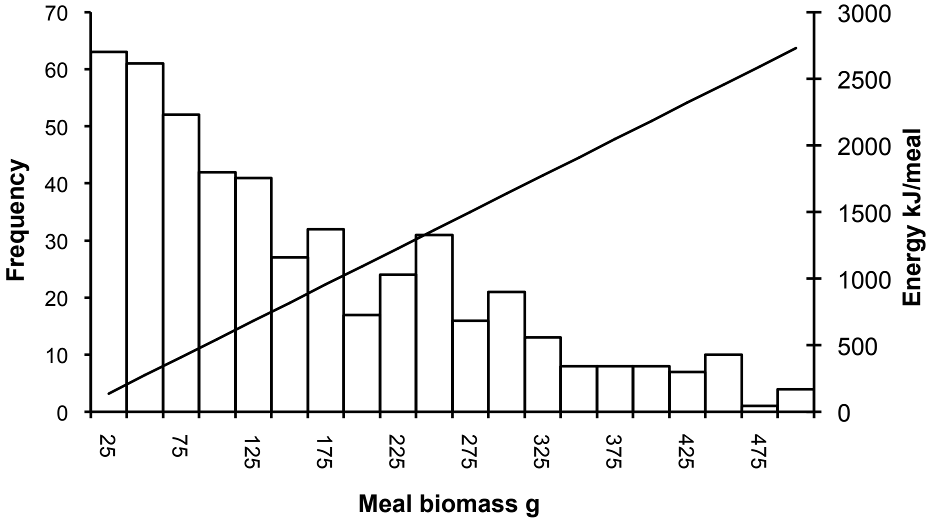

Table 3. The frequency of occurrence of prey taxa at all colonies and prey taxa consumed across all colonies (standardised for colony) in each season.

	Colony								Season			
Species	Granite	Greenly	Olive	Pearson	Reevesby	Troubridge	West	Franklin	Autumn	Winter	Spring	Summer
Acanthaluteres spilomelanurus	-	10.5	-	1.5	16.9	11.9	-	-	2.5	6.8	15.6	1.8
Aldrichetta forsteri	-	-	-	0.8	-	0.5	-	-	-	1.1	-	-
Arripis georgiana	-	94.7	-	5.3	11.7	8.5	42.9	-	-	3.7	27.0	5.4
Atherinason hepsetoides	-	-	-	-	37.7	2.4	-	-	3.8	10.0	7.2	-
crab megalopa larvae	-	15.8	-	27.1	2.6	0.5	-	-	2.5	1.1	16.2	19.6
Emmelichthys nitidus	-	57.9	71.4	48.1	10.4	4.3	14.3	36.4	2.5	11.1	29.3	60.7
Engraulis australis	100	15.8	100	86.5	79.2	81.0	100	100	68.4	91.6	71.3	98.2
Hippocampus abdominalis	-	-	-	0.8	-	-	-	-	1.3	-	-	-
Hyporhamphus melanochir	56.3	63.2	-	45.9	19.5	36.5	42.9	-	55.7	16.8	46.7	41.1
Isopods	-	-	-	0.8	3.9	1.9	-	-	5.1	1.1	1.2	-
larval fish	6.3	-	-	7.5	26.0	12.3	-	-	7.6	7.4	22.2	-
nematodes	-	5.3	-	3.8	2.6	1.4	-	9.1	2.5	3.2	1.2	5.4
Nototodarus gouldi	18.8	84.2	-	47.4	5.2	14.2	14.3	31.8	25.3	11.1	27.5	66.1
Parapriacanthus elongatus	-	-	-	1.5	9.1	25.1	-	-	25.3	9.5	13.8	1.8
Parequula melbournensis	-	-	-	-	9.1	-	-	-	-	-	4.2	-
plastic	-	-	-	0.8	-	-	-	-	1.3	-	-	-
prawn spp	-	-	-	-	1.3	0.5	-	-	2.5	-	-	-
Pseudocyttus maculatus	-	-	-	0.8	-	-	-	-	-	-	-	1.8
Pseudophycis sp	6.3	-	-	-	-	-	-	-	-	-	0.6	-
Sardinops sagax	50.0	-	-	30.8	50.7	62.6	57.1	40.9	31.7	72.6	36.5	16.1
Seagrass	-	-	-	-	1.3	0.5	-	-	1.3	1.1	-	-
Scomber australasicus	-	-	-	-	-	-	6.0	-	-	-	0.6	-
Scomberesox saurus	-	5.3	-	14.3	3.9	3.8	-	9.1	29.1	3.7	0.6	3.6
Scorpis lineolata	-	-	-	0.8	-	-	-	-	-	-	0.6	-
Seriolella brama	-	-	-	0.8	-	-	-	-	1.3	-	-	-
shells and cuttlebone	-	-	-	0.8	6.5	5.7	-	-	5.1	4.2	3.6	-
fish sp 1.	-	-	-	9.0	14.3	15.6	-	-	31.7	10.5	6.6	-
fish sp 2.	-	-	-	-	1.3	-	-	-	-	-	0.6	-
fish sp 3.	-	-	-	-	1.3	-	-	-	-	-	0.6	-
fish sp 4.	-	-	-	7.5	-	-	-	-	-	5.3	-	-
Spratelloides robustus	-	-	-	-	13.0	44.6	14.3	-	39.2	33.2	6.6	-
Stimatopora argus	18.8	-	-	-	2.6	10.4	-	-	3.8	3.7	10.2	-
Trachurus declivus	-	-	-	0.1	-	0.1	-	-		-	-	-
unknown fish	25.0	36.8	-	9.0	13.0	13.7	28.6	4.6	21.5	9.5	15.6	7.1

Of the 26 prey species, Australian anchovy was the most frequently consumed (mean FO 82 % samples per colony) (Table 3.). Anchovy was the only prey species found at all colonies. With the exception of Greenly Island, anchovy accounted for 39 – 92 % of prey items and 46 – 95 % of all identifiable biomass consumed (Table 4 and 6). In comparison, at Greenly Island, anchovies only accounted for 1.7 % of prey items and 2 % biomass. Across all colonies, anchovies contributed 147 g (74 - 75 % biomass) per daily meal in both winter and summer, where as anchovies only contributed 30 g (28 %) in spring and 51 g (33 %) in autumn. Of the less common prey species, southern sea garfish *Hyporhamphus melanochir* was present at all colonies except Olive and Franklin Islands, in 19 – 63 % of samples. Despite low numerical abundance (2 - 11 %), garfish was the second most important prey species across all colonies (biomass 13%), particularly in autumn (31 % vs < 19 % other seasons), because fish were large. Except Greenly and Olive Islands, sardines were also caught frequently (FO 30 – 63 %) but they only accounted for 6 % of the biomass. Redbait *Emmelichthys nitidus,* blue sprat *Spratelloides robustus,* Gould's squid *Nototodarus gouldi*, tommy rough *Arripis Georgiana,* slender bullseye *Parapriacanthus elongatus,* deepwater hardyhead *Atherinason hepsetoides*, sauries *Scomberesox saurus*, larval fish and sygnathids were also common at particular sites in particular seasons (FO up to 45 – 95 %) but their combined contribution was small (< 14 % biomass). Only a small percent of prey were not identified (0.5 – 7 %).

Eroded mollusc shells were found in 35 (5 %) samples of which 77 % were from female penguins. A total of 35 (5 %) samples contained hard plastic, of which four from Pearson Island and one from Troubridge Island revealed up to six pieces. No significant day-to-day variation existed in the biomass, size, or FO of the three most common prey species at Troubridge Island: anchovy, blue sprat and sardine (*n* samples used per day = 7, 3, 2, 6, 5, 5, 8, $P > 0.05$ in all cases) (Table 5).

Table 4. The numerical abundance (% NA) of prey taxa consumed at all colonies prey taxa consumed across all colonies (standardised for colony) during each season.

	Colony								Season			
Prey taxa	Granite	Greenly	Olive	Pearson	Reevesby	Troubridge	West	Franklin	Autumn	Winter	Spring	Summer
Acanthaluteres spilomelanurus	-	1.0	-	0.1	0.1	1.1	-	-	0.1	0.2	0.2	>0.1
Aldrichetta forsteri	-	-	-	0.8	-	0.5	-	-	-	-	-	-
Arripis georgiana	-	64.9	-	0.2	1.4	0.7	15.3	-	-	0.4	9.3	0.2
Atherinason hepsetoides	-	-	-	-	9.6	0.2	-	-	0.1	2.5	1.8	-
crab megalopa larvae (groups of 10)	-	0.6	-	7.1	0.2	0.1	-	-	0.5	0.7	6.8	5.5
Emmelichthys nitidus	-	7.7	22.0	9.2	0.6	0.5	2.0	1.6	0.0	1.2	6.5	7.1
Engraulis australis	66.5	1.7	78.0	49.5	39.7	39.9	49.7	92.2	27.7	64.7	24.4	65.1
Hippocampus abdominalis	-	-	-	0.1	-	-	-	-	0.2	-	-	-
Hyporhamphus melanochir	11.1	3.5	-	5.3	5.2	6.6	7.1	-	15.8	1.1	6.2	4.0
larval fish (groups of 10)	2.0	-	-	5.2	17.9	9.3	-	-	2.4	4.4	17.2	-
Nototodarus gouldi	2.2	19.7	-	7.3	1.2	1.7	2.4	3.6	3.9	1.3	4.0	12.3
Parapriacanthus elongatus	-	-	-	0.1	1.8	5.7	-	-	7.2	0.7	3.8	>0.1
Parequula melbournensis	-	-	-	-	0.9	-	-	-	-	-	0.4	-
prawn species	-	-	-	-	0.1	-	-	-	0.1	-	-	-
Pseudocyttus maculatus	-	-	-	0.1	-	-	-	-	-	-	-	0.2
Pseudophycis sp	0.5	-	-	-	-	-	-	-	-	-	0.1	-
Sardinops sagax	6.6	-	-	4.3	7.6	18.1	13.0	1.9	4.5	13.6	13.4	0.8
Scomber australasicus	-	-	-	-	-	-	2.0	-	-	-	0.1	-
Scomberesox saurus	-	0.1	-	5.2	2.7	0.1	-	0.2	8.8	1.2	>0.1	0.1
Scorpis lineolata	-	-	-	-	-	-	-	-	-	-	>0.1	-
Seriolella brama	-	-	-	0.2	-	-	-	-	0.3	-	-	-
fish sp 1.	-	-	-	0.5	2.4	3.0	-	-	10.9	3.0	3.0	-
fish sp 2.	-	-	-	-	1.2	-	-	-	-	-	>0.1	-
fish sp 3.	-	-	-	-	1.2	-	-	-	-	-	>0.1	-
fish sp 4.	-	-	-	0.1	-	-	-	-	-	>0.1	-	-
Spratelloides robustus	-	-	-	-	0.9	8.1	7.1	-	12.3	3.7	0.9	-
Stimatopora argus	4.0	-	-	-	1.0	0.2	-	-	2.0	0.3	0.1	-
Trachurus declivis	-	-	-	0.3	-	0.1	-	-	0.3	0.1	0.1	0.1
unknown spp.	7.1	1.0	-	4.5	4.3	4.3	1.3	0.5	3.1	1.1	1.8	4.6

Table 5. The daily frequency of occurrence (FO), mean proportional biomass, mean fish size and mass ± S.E. of anchovies, blue sprat and sardines in little penguin diets at Troubridge Island from 7th-13th July 2004.

Variable	*n* days	anchovy	blue sprat	sardine
FO %	7	100 ± 0	79.3 ± 7.0	75.3 ± 6.8
Proportional biomass of the meal %	7	79.5 ± 2.4	8.4 ± 2.6	6.9 ± 1.6
Mean fish size (mm)	7	84.0 ± 1.4	74.6 ± 1.2	49.8 ± 1.8
Mean fish mass (g)	7	5.7± 0.4	3.8 ± 0.2	1.6 ± 0.2

Table 6. The estimated relative biomass (% ERB) of identified prey taxa consumed at all colonies and prey taxa consumed across all colonies (standardised for colony) during each season.

	Island Colony								Season			
Prey taxa	Granite	Greenly	Olive	Pearson	Reevesby	Troubridge	West	Franklin	Autumn	Winter	Spring	Summer
Acanthaluteres spilomelanurus	-	0.4	-	0.0	0.4	3.1	-	-	0.5	1.2	2.5	0.0
Arripis georgiana	-	59.2	-	0.1	0.8	0.8	8.8	-	-	0.5	7.8	0.1
Atherinason hepsetoides	-	-	-	-	9.5	0.1	-	-	0.3	2.0	2.2	-
crab megalopa larvae	-	0.1	-	5.0	0.0	-	-	-	0.1	0.0	3.3	1.9
Emmelichthys nitidus	-	6.4	11.3	6.6	1.0	0.5	5.0	1.3	0.8	0.6	5.3	4.7
Engraulis australis	75.5	2.0	88.8	57.7	48.1	47.0	60.2	94.8	33.0	74.9	28.2	73.7
Hippocampus abdominalis	-	-	-	0.8	-	-	-	-	1.3	-	-	-
Hyporhamphus melanochir	16.0	17.3	-	18.0	11.5	14.6	4.5	-	31.7	2.6	19.7	11.9
larval fish	3.3	-	-	1.0	21.1	6.4	-	-	1.4	5.4	12.2	-
Nototodarus gouldi	1.9	14.6	-	5.2	0.9	1.0	2.5	2.5	3.5	0.9	3.0	7.0
Parapriacanthus elongatus	-	-	-	0.1	1.7	4.4	-	-	5.7	0.6	2.9	0.0
Parequula melbournensis	-	-	-	-	0.1	-	-	-	-	-	0.0	-
prawn species	-	-	-	-	>0.1	-	-	-	>0.1	-	-	-
Pseudocyttus maculatus	-	-	-	0.1	-	-	-	-	-	-	-	0.1
Psuedophycis sp	0.4	-	-	-	-	-	-	-	-	-	0.0	-
Sardinops sagax	1.0	-	-	2.3	4.0	12.2	1.8	1.4	2.0	7.6	9.7	0.6
Scomber australasicus	-	-	-	-	-	-	4.8	-	-	-	0.2	-
Scomberesox saurus	-	0.0	-	3.3	-	0.0	-	-	5.6	0.0	0.0	-
Spratelloides robustus	-	-	-	-	0.8	7.9	12.4	-	12.7	3.3	1.1	-
Stimatopora argus	1.9	-	-	-	0.2	1.9	-	-	1.2	0.3	1.7	-

A total of 27,543 otoliths were extracted from all stomach samples for identification. From the 13,983 left otoliths, 13,512 were measured and identified as one of 16 fish species. From the 592 cephalopod beaks, 103 were also measured (Table 7). The mean size and biomass of prey was 80.4 ± 0.3 mm and 5.4 ± 0.05 g. The largest item was a garfish measuring 328 mm with a mass of 112 g. The average ages of sardine, blue sprat and anchovy were 3, 6 and 8 months respectively and all were younger than 2 years. Garfish averaged 2.3 years but fish as young as four months old were consumed (Table 7). Prey length of the most abundant prey species (anchovy, garfish, sardine, blue sprat, bullseye, tommy rough, redbait and hardyhead) was not correlated with penguin mass, sex, bill depth or bill length ($P > 0.05$ in all cases).

Table 7. Summary of fish lengths (*SL* standard length, *TL* total length, *FL* fork length, * bend of upper mandible to posterior of medial caudal-fin ray) and masses estimated from measurements of otoliths that were removed from little penguin stomach samples at all colonies. The ages of four species (anchovy, sardine, blue sprat and garfish) were estimated from fish lengths. The reference column refers to data and equations that were used to estimate fish lengths, mass and ages (see footnote).

		Length (mm)			Mass (g)		Age (d)		Reference
Prey species	n	Mean ± S.E.	Range		Mean ± S.E.	Range	Mean ± S.E.	Range	
Engraulis australis	7983	84.09 ± 0.15	2.13 - 140.72	SL	6.00 ± 0.03	0.43 - 31.22	254.31 ± 0.58	77.36 - 480.90	1, 2
Sardinops sagax	1962	51.52 ± 0.4	14.45 - 138.97	*SL*	1.95 ± 0.06	0.30 - 29.7	84.79 ± 1.23	29.98 - 669.37	1, 3 (for samples from Troubridge, West and Granite Islands), 4 (for samples from other islands)
Spratelloides robustus	664	71.95 ± 0.32	44.9 - 151.19	*TL*	3.42 ± 0.08	0.68 - 39.79	172.78±0.97	89.46 - 413.62	5
Parapriacanthus elongatus	639	89.65 ± 0.68	40.8 - 141.76	*SL*	3.48 ± 0.05	0.70 - 7.11			6.
Arripis georgiana	601	64.54 ± 0.33	29.29 - 105.62	*FL*	3.14 ± 0.04	0.93 - 11.95			7.
Emmelichthys nitidus	587	70.41±0.55	41.94 - 137.88	*FL*	3.45 ± 0.10	0.52 - 29.14			1
Atherinason hepsetoides	551	84.85±0.41	44.26 - 113.15	*SL*	3.14 ± 0.03	0.32 - 5.12			1
Hyporhamphus melanochir	397	198.78 ± 2.78	58.1 - 327.85	*SL*	23.17 ± 0.94	0.16 - 111.92	858.94 ± 2 6.71	121.84 - 3477.80	8
Scomberesox saurus	61	83.31 ± 2.86	42.06 - 132.85	*FL**	2.46 ± 0.24	1.24 - 8.43			9
Acanthaluteres spilomelanurus	31	49.56 ± 3.09	19.58 - 76.55	*SL*	3.15 ± 0.41	0.18 - 8.34			1
Trachurus declivus	6	130.72 ± 3.03	120.58 - 143	*FL*	25.62 ± 1.79	20.21 - 33.2			1

References for Table 6. *OL* = otolith length, Wt = fish mass.

1. Furlani *et al.* 2007, 2. *age* = (*SL*-20.51)/0.25 (from Dimmlich and Ward 2006), 3. *FL* = 0.25*age* + 29.87 (r^2 = 0.66, *n*= 296, Gulf St Vincent, from Ward *et al.* 2005), 4. *FL*= 0.44*age* + 20.84 (r^2 = 0.71, *n*=257, Spencer Gulf, from Ward *et al.* 2005, 5. *age* =(*FL*-16.973)/ 0.3211, where *FL* =51.602 x $Wt^{0.2893}$ (*n*= 1211, r^2 = 0.97, Gulf St Vincent, P. Rogers unpublished data), 6. *SL*=27.3 x $OL^{0.95}$, 6.*Wt* =-3.4+10.87 x 10^{-2} x *SL* (this study), 7. *FL*= 24.848 x *OL* + 0.602 *Wt* = 5E-06 x $FL^{3.1872}$ (*n*= 10, r^2 = 0.9897, *O* =2.66–5.34 mm, *FL*=67.61-137.12 mm, *Wt*=3.2-30.8 g, South Aust, samples from SARDI), 8. *SL* = 80.484Ln(*age*) - 328.44 (Gulf St Vincent, estimated from Ye *et al.* 2002), Furlani *et al.* 2007, 9. *FL* = (95.079 x *OL*)-36.298, *Wt* = 0.0018 x ($(FL)^2$))-(0.2508 x (*FL*))+9.9783, *Wt* = 0.0018 x ((($95.079 \times OL)-36.298)^2$) - (0.2508 x ((95.079 x *OL*)-36.298)) + 9.9783 (*n* = 21, r^2 = 0.9953, *OL* range = 0.95–2.77 mm, *FL* range = 54–230 mm, *Wt* range 0.5–48.83 g, samples from Greenly Island 2005, this study).

At Troubridge Island, penguins consumed anchovies and sardines that significantly decreased in otolith size throughout the year in 2005 ($n = 608$, $r^2 = 0.2$, $P < 0.001$ and $n = 920$, $r^2 = 0.13$, $P < 0.001$ respectively). The same trend for anchovies in 2006 was only significant to 0.094 ($n = 51$, $r^2 = 0.1$, $P = 0.094$) (Fig. 3).

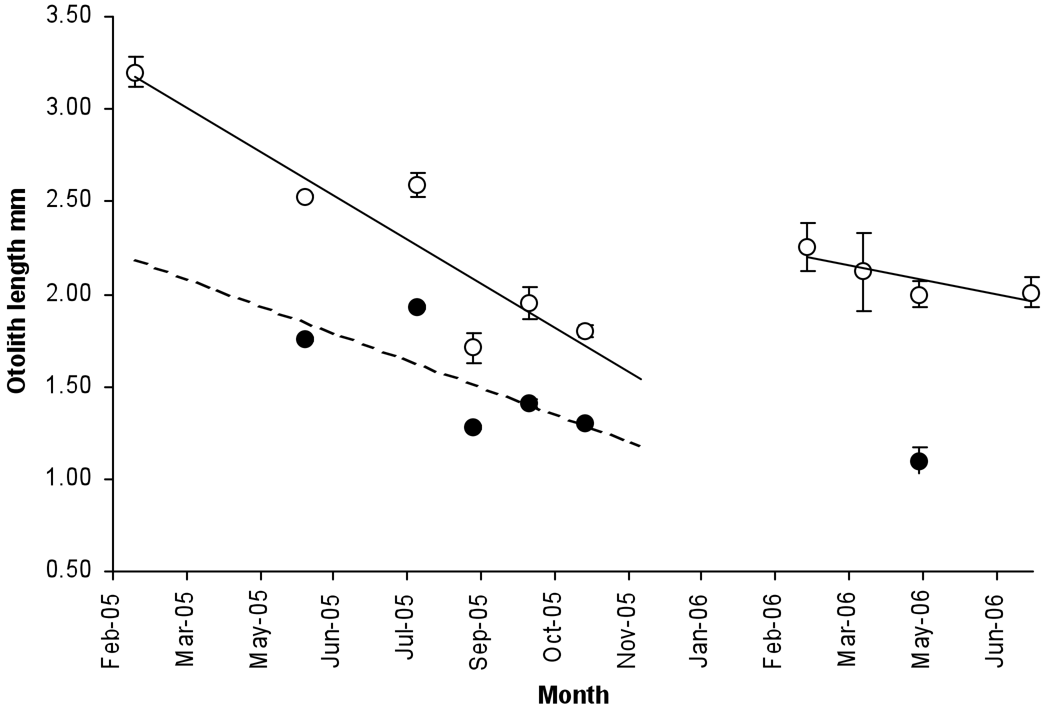

Figure 3. The mean (± S.E.) otolith length of anchovies (open circles with solid trend line) and sardines (closed circles with dashed trend line) retrieved from diet samples of little penguins at Troubridge Island in 2005 and 2006. No trend line for sardines in 2006 is displayed because only one month of data was available.

The colony niche overlap indices based on NA and ERB indicated that colony diets were not significantly different ($P > 0.50$) because of the high abundance of anchovies. Exceptions included Greenly Island ($P < 0.32$) as well as Olive and Franklin Islands, which were very similar to each other ($P > 0.80$), but dissimilar to the diets from Troubridge and Reevesby Islands ($P > 0.43$).

The MRT revealed that only 31.5 % of the variance in the prey species composition and biomass of individual diets was explained by environmental, ecological and biological parameters. The effects of season explained the greatest difference (14 %). The samples collected in winter and summer, which had the highest proportional anchovy biomass, were split from those collected in autumn and spring. Sea-surface temperatures and breeding parameters accounted for the remaining 16.5 % variance.

At the colony level, mean anchovy biomass correlated weakly but significantly with the proportion of active nests containing eggs in the colony at the time of sampling (n = 36 sampling trips, r^2 = 0.1 P = 0.046), but not those containing chicks (P > 0.1). Sea swell was not related to anchovy biomass (P > 0.1). Anchovy biomass (g) and proportional anchovy biomass (%) were both significantly correlated with larger meal masses (n = 493 meals, r^2 = 0.1 and 0.4, P < 0.001 in both cases). Anchovy biomass was also very weakly, but significantly negatively correlated with male and female body mass (r^2 = <0.1 males and females, both P < 0.05), and female body condition (mass/*BD* where *BD* was used as proxy for skeletal size, r^2 = <0.1, P = 0.012), but not male body condition (P > 0.05).

Of the species that were analysed for nutrient content, anchovy provided the highest calorific value (5.9 $kJ.g^{-1}$ wet mass), lipid percentage (5 % wet mass) and the second highest proportion of protein (20 % wet mass) (Table 8 and 9). The mean calorie content of meals from all colonies was 804 ± 32 kJ, of which anchovy comprised 62 ± 10 % (or 70 ± 7 % kJ if Greenly Island was excluded). Despite garfish being energy poor (3.5 $kJ.g^{-1}$ wet mass), it was consumed in sufficient amounts to contribute 9 ± 3 % of the mean daily calorie content. Sardine contributed 3 ± 1 % and other prey species each contributed less than 4 %. The mean calorific content of the average diet was 5.46 $kJ.g^{-1}$ wet mass and daily calorie content ranged from 32 to 4506 kJ.

Table 8. Summary table of numbers and weights of prey species samples used for the nutritional analyses.

Species	Mean wet weight g ± S.E.	Wet weight range g	Mean dry weight g ± S.E.	Range dry weight	Samples (*n* individual fish per sample)
Acanthaluteres spilomelanurus	3.8 ± 0.2	3.1-4.6	0.8 ± 0.0	0.6-0.9	1(7)
Atherinason hepsetoides	3.6 ± 0.1	3.3-4.0	0.9 ± 0.0	0.7-1.0	1(5)
Emmelichthys nitidus	49.3 ± 0.9	46.6-50.8	14.1 ± 0.5	13.4-15.7	4(1,1,1,1)
Engraulis australis	6.4 ± 0.1	5.7-6.9	1.6 ± 0.0	1.5-1.8	1(10)
Etrumeus teres	10.2 ± 0.4	9.3-11.3	2.5 ± 0.1	2.3-2.8	4(1,1,1,1)
Hyporhamphus melanochir	57.9 ± 2.5	49.9-72.3	14.7 ± 1.6	11.8-18.7	1(9)
Nototodarus gouldi	33.5 ± 12.3	17.0-57.4	8.7 ± 3.2	4.3-14.8	3(1,1,1)
Parapriacanthus elongatus	4.9 ± 0.2	3.7-6.0	1.1 ± 0.0	0.8-1.3	1(10)
Paraquula melbournensis	8.5 ± 2.2	2.3-25.5	2.6 ± 0.8	0.5-9.2	6(1,1,7,1,1,1)
Sardinops sagax	17.0 ± 3.0	12.3-3	4.4 ± 0.9	3.0-9.0	6(1,1,1,1,1,1)
Scomberesox saurus	16.9 ± 3.8	0.5-48.8	4.6 ± 1.1	0.1-14.2	13(1,1,1,1,1,1,1,1,1,1,1,1,9)
Sepioteuthis australis	49.0 ± 7.7	24.5-78.0	10.4 ± 2.1	1.4-18.8	7(1,1,1,1,1,1,1)
Spratelloides robustus	1.5 ± 0.2	1.0-1.7	0.3 ± 0.0	0.3-.4	1(3)
Upeneichthys vlamingii	11.1 ± 2.6	2.5-32.8	2.7 ± 0.7	0.5-8.2	8(1,1,1,3,1,1,1,1)

Table 9. The calorific value (kJ.g^{-1}) of each prey species and the proportional lipid and protein composition. dm =dry mass; wm = wet mass. Species are ordered by kJ.g^{-1} dm.

Species	kJ.g^{-1}dm	kJ.g^{-1}wm	% lipid	% protein
Engraulis australis	23.26	5.88	20.54	79.72
Etrumeus teres	21.52	5.04	16.60	78.73
Paraquula melbournensis	21.42	5.01	16.85	77.72
Spratelloides robustus	20.68	4.63	18.46	70.47
Upeneichthys vlamingii	20.07	4.62	15.30	73.83
Sardinops sagax	19.79	4.84	11.24	80.80
Atherinason hepsetoides	19.62	4.5	13.29	75.61
Sepioteuthis australis	19.10	4.50	8.09	83.71
Parapriacanthus elongatus	18.93	4.10	13.05	72.52
Acanthaluteres spilomelanurus	18.87	3.35	14.10	70.02
Nototodarus gouldi	18.08	4.69	8.04	78.47
Hyporhamphus melanochir	18.07	3.51	8.22	78.03
Scomberesox saurus	17.68	4.95	9.29	73.73
Emmelichthys nitidus	17.43	4.53	10.58	69.74

Discussion

A reliance on anchovies

Little penguins frequently consume clupeoid fish species across their distribution but in South Australia little penguins rely on anchovies relatively more (67 % vs 0.1 – 16 % biomass, and 92 % vs 2 – 30 % FO in Tasmania, Victoria and Western Australia) (Klomp and Wooler 1988, Gales and Pemberton 1990, Cullen *et al.* 1992, Eberle 2003). In comparison, sardines were once a more common prey at Phillip Island, Victoria (Montague and Cullen 1988) although they have reduced in penguin diets in recent decades (Chiaradia *et al.* 2003). Across South Australia, the consistently high abundance of anchovies in diets also reflects the abundance of anchovy larvae and eggs in gulf and shelf waters (Ward *et al.* 2001a, Ward *et al.* 2006). Sardine eggs and larvae are just as common, if not more so (Ward *et al.* 2001b). The spawning biomass of adult sardines (~269,000 t, Ward *et al.* 2003) in the eastern GAB gulfs and shelf waters is about twice that of anchovies (126,000 t, Dimmlich *et al.* 2009). If egg and larvae, and/or spawning biomass proportions of both fish species were reflected in juvenile abundances, then penguins appeared to be selecting anchovies. Juvenile anchovies also have a higher energy value than sardines, providing a possible explanation for prey selectivity in South Australian little penguins.

Penguins capture juvenile anchovies throughout the year in South Australia, but the greatest dietary proportions and biomasses were in winter (when sea surface temperatures was lowest) and in early summer. These seasons coincide with the peak breeding and moulting periods respectively, when energy budgets for little penguins generally increase. In the region's offshore waters and gulfs, anchovy spawning peaks during summer (Dimmlich *et al.* 2004). The juvenile fish grow to the preferred prey size-range of penguins (60 - 90 mm) within 5 - 9 months (Dimmlich and Ward 2006). This growth period corresponds with late autumn to spring, when adult penguins are feeding chicks. The high sea swell of winter conditions also does not affect diving penguins from successfully catching anchovies, unlike the plunge-diving strategies used by other local seabirds such as terns, which capture less prey in rough conditions (McLeay pers comm). The availability of anchovies at particular times of the year may underpin the timing of breeding.

Around the world, anchovy species are important prey for several seabirds including African penguins *Spheniscus demersus*, Cape gannets *Sula capensis* , brown pelicans, *Pelecanus occidentalis californicus,* Cape cormorants *Phalacrocorax capensis* and Guanay cormorants *P. bougainvilii* (Crawford and Shelton 1978, Anderson et al. 1982, Furness and Monaghan 1987, Crawford and Dyer 1995). Abundant anchovies appear to be important for the onset of little penguin breeding in South Australia, indicated by the high proportion of eggs in the colony when anchovy biomass peaked in penguin diets. This supports findings at Phillip Island, where the late arrival of both sardines and anchovies within penguin foraging ranges coincided with a late onset of breeding and poor fledging success (Cullen *et al.* 1992, Hobday 1992). Breeding at Phillip Island, extends from spring to summer (October-February) and is directly followed by moulting when prey are still abundant (Robinson *et al.* 2005). In comparison, because anchovies are available to South Australian colonies throughout the year, the breeding period is more protracted (April-November), asynchronous within and between colonies, and double brooding is common (Johnson and Wiebkin 2008).

Although anchovy biomass appears to prompt the onset of breeding, individual penguin mass (particularly females) and body condition (mass/*BD*) (for females) was lower when they ate more anchovies. This is unlikely to be a causal relationship. Penguin body masses are known to reduce during the breeding season because the energetic demands of laying eggs (for females), incubating eggs and provisioning for chicks increase (Klomp and Wooler 1988, Green *et al.* 2007).

Prey selection based on size and abundance is consistent with predictions of classical optimal foraging theory, where choice of prey is primarily influenced by profitability of prey items (energy and handling time; Stephens and Krebs 1986). Despite evidence of little penguins selecting anchovies, which suggests that these fish were profitable, particular prey sizes were probably not selected. Anchovy size was not correlated with penguin sex, body mass or bill size, unlike those at Phillip Island

(Shaw *et al.* 2007). My data suggest that little penguins are able to capture and kill the same sized anchovies in this region, as well as much larger garfish, so the range of prey sizes for anchovies was not restricted by the capacity of little penguins to take larger prey. While it is not known whether larger prey can be caught, processed or digested with comparable efficiency as smaller prey, penguins readily consumed prey of varying sizes throughout the year at Troubridge Island. For these reasons prey size probably does not drive bill size or body size variation in the eastern GAB.

At Troubridge Island, where sampling frequency was highest, the decrease in otolith sizes of both anchovy and sardine may suggest that cohorts of smaller fish were moving into the penguin foraging areas as the year progressed, and/or that larger fish were moving out. This supports evidence of age or size specific anchovy migration in South Africa and Europe (Cruickshank 1990, Basilone *et al.* 2004), and in South Australia where anchovies move out of the nursery areas in the gulfs and then swim off-shore where they may live up to 5 years (Dimmlich *et al.* 2006, Dimmlich *et al.* 2009).

Meal masses

Water, sodium and energy turnover studies indicate that adult little penguins require 222 g (wet mass) or 1418 kJ per day. They also require an additional 236 g (wet mass) or 1460 kJ pr day to maintain the growth of a medium to large chick (Green *et al.* 1988). Penguins in captivity at Taronga Zoo generally eat about a third of their body weight (approx. 300g) per day (E. Walraven, pers. comm. Taronga Zoo in NPWS 2000, in NPWS 2000). In my study, the mean estimated daily meal biomass (147 g) and energy content from pooled samples (804 kJ) was considerably less than the requirements for an adult alone, (33 % and 43 % respectively), due to digestion that occurs whilst foraging. Similarly, stomach content masses (wet meal masses) from other regions were much smaller than the required energy (Tasmania: mean 30 – 47 g, Victoria: 80 g, Western Australia: 57 g) (Montague 1982, Klomp and Woller 1988, Gales and Pemberton 1990). However, in support of Green *et al.* (1988) my samples illustrated that meals of up to 497g (or 432 g wet mass), containing 4506 kJ were achievable.

Penguins that were not provisioning chicks had no need to return to the colony with food in their stomachs, which is reflected by the high number of small meals collected, particularly in the non-breeding periods. Meals from little penguins in Tasmania can be completely digested within 8 to 16 hours and 20 – 60 % of fish otoliths can be digested in 4 to 8 hours (Gales 1988). Cullen *et al.* (1992) found species-specific differences in the degree to which otoliths had been digested, either reflecting time since capture or differential digestibility rates, and these were relatively low for anchovy and garfish. In contrast, this study found that anchovy and garfish otoliths exhibited high rates of digestion compared with sardines (ratios of condition Class 3 : 1; 1.74 for anchovies, 1.06 for garfish vs 0.33 for sardines). My method of estimating otolith erosion is supported at least for sardines because erosion rates were similar to those found in laboratory experiments (Caines 2005). Assuming no species differences in time-of-capture across colonies, the relative proportions of anchovy and garfish in little penguin stomachs are therefore likely to be under-represented in the diet composition.

Based on the daily energy requirements for adults throughout the year and for chicks during the seven weeks of growth per year (Green *et al.* 1988), the minimum population of little penguins in South Australia (40,000 individuals, Copley 1996, plus an additional 57 % juvenile penguins, Dann and Cullen 1990, and 0.7 chicks that fledge per breeding pair, (mean breeding success for 4 islands in SA, Chapter 6) consume 3.3 x 10^{10} kJ or 5,688 tonnes per year, of which 2.4 x 10^{10} kJ or 3,811 tonnes is juvenile anchovy. Copley (1996) estimated the state population to be 40,000 – 100,000 breeding birds prior to 1996, but many colonies in SA have declined and recent surveys now support the lower estimate (Wiebkin 2011). Because little penguins are central-place foragers, most of this prey is consumed within discreet foraging areas around each colony (i.e. within 20 km of the colony during chick provisioning). Within these coastal areas little penguins are therefore very significant consumers of anchovy.

Specialist strategies

Little penguins across South Australia are not the generalist predators they have been labelled in other regions (Cullen *et al.* 1992), but rather, with the exception of

Greenly Island, they exhibit a preference for anchovies, much like the single-prey species preferences of penguins living in higher latitudes (Lynnes *et al.* 2004). Despite the apparent abundance of sardines in the region (Ward *et al.* 2003, Dimmlich *et al.* 2009) and the availability of a diverse suite of prey comparable to other locations (Klomp and Wooller 1988, Gales and Pemberton 1990, Montague 1982), we can speculate that little penguins target anchovies across most colonies, seasons and years. Being anchovy specialists, these little penguins may benefit from well-practised, reliable and anchovy-targeted feeding strategies, optimal digestive performance for one prey (Hilton *et al.* 2000) and their breeding may benefit from being asynchronous and prolonged to buffer fluctuations in prey availability. These characteristics and a reliance on anchovies have potential management implications for little penguin populations if ecological conditions change through fishing pressure, climate change, competition from other avian predators or mass mortality events (Collins *et al.* 1999, Chiaradia *et al.* 2003, Dann *et al.* 2000, Ward *et al.* 2001b).

Other studies have shown that little penguins can change their diets in response to changes in prey species availability (Cullen *et al.* 1992, Chiaradia *et al.* 2003, Chiaradia *et al.* 2010). In South Australia, if anchovies became less abundant across the region, penguins would most likely rely more on garfish and sardines because diet data suggests they are widespread and frequently consumed across South Australia, and they are common in the diets of little penguins from other regions (Klomp and Wooller 1988, Chiaradia *et al.* 2003). Futhermore, because garfish were the second most important prey species (by biomass and energy contribution), and because they were considerably larger than all other prey (also the case in Victoria, Cullen *et al.* 1992), penguins may exhibit a high degree of selectivity for garfish. However, garfish are relatively less energy dense compared to favoured prey and penguins do not target them during the winter breeding season, suggesting they may not be available in sufficient biomass to support chick growth at this time.

The non-prey stomach contents found in this study also reveal insights into reproductive and foraging strategies as well as anthropogenic pollutants. Of the non-prey items ingested, partly digested mollusc shells were common in female samples, probably ingested prior to laying as a source of calcium for eggshell development

(Graveland and Berends 1997), but they may also be used as ballast to compensate for buoyancy whilst diving (Kato *et al.* 2006). Buoyant plastic fragments, which are regularly found in the diets of 44 % of seabird species (Hutton 2004), indicate some surface foraging in little penguins.

Competition with fisheries and implications of ecological change

Seabird diets have been linked to variation in prey abundance and recruitment resulting from fishing pressure or mass fish mortality events (Monaghan *et al.* 1989, Dann *et al.* 2000, Litzow *et al.* 2000, McLeay 2009). Increases in sardine harvest and mass mortalities of sardine in Victoria have coincided with decreases in clupeoids in penguin diets, increases in adult mortality and reductions in breeding success at Phillip Island (Cullen *et al.* 1992, Neira *et al.* 1999, Dann *et al.* 2000, Chiaradia *et al.* 2003). Little data exists for the effects of sardine mass mortalities on South Australian little penguin populations (Dann *et al.* 2000) but two recent mass mortality events facilitated the expansion of anchovy distribution and biomass (Ward *et al.* 2001a), potentially benefiting local little penguin populations. The South Australian sardine fishery currently harvests up to 39, 000 tonnes of sardine per year (from a spawning biomass of ~220,000 t, Ward *et al.* 2001b) and the fishery reports < 1 % anchovy by-catch (Ward *et al.* 2008). Based on this, little penguins are unlikely to be in direct competition with the fishery for anchovies, however, a quota of 1,000 tonnes of anchovy was allocated to SA sardine fishers in 2011. This is a small proportion of the estimated spawning biomass of anchovies in the eastern GAB (~126,000 t, Dimmlich *et al.* 2009), but any future expansion of this fishery should be carefully evaluated and ecological assessments should be based on dependent species such as little penguin.

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Chapter 5: Does the diving behaviour of little penguins differ at sites where their primary prey can access different depths?

Abstract

Little Penguin colonies in the eastern Great Australian Bight are located in different marine environments from shallow gulfs to deeper shelf water habitats. Differences in foraging behaviour of little penguins are expected to reflect these contrasting environments. I studied the dive behaviour of little penguins at two sites characterised by shallow (gulf, mean 20 m) and deep (shelf, mean 61 m) habitats. Little penguins from both sites consumed the same principal prey species, anchovies (in > 80 % of diet) and they consumed similar volumes of food per day. Penguins from the deep water site made more dives and spent more time diving each day, partly because their prey (principally anchovies) were smaller. However, mean dive depth, diving period, dive duration, descent and bottom time did not differ between the sites. The seafloor around the shallow environment was well within the penguins' diving capability, nevertheless they foraged at mid-water depths. Penguins from the deep-water site also foraged at similar mid-water depths because the sea floor was too deep for them. Anchovies are a dominant species in the small pelagic fish assemblage in gulf and shelf waters of South Australia and anchovy distribution may determine the distribution and abundance of little penguin populations in SA. Moreover, the distribution of anchovies in the water column (surface schooling), likely underpins the dive behaviour of little penguin at both sites.

Key words: penguin, *Eudyptula minor*, diving, foraging, anchovy, water depth.

Introduction

Diving behaviour of marine predators is influenced by physiology, prey distribution and features such as seafloor depth. Many studies focus on the relationship between diving depth and the proximity of seafloor because prey type is often associated with bathymetry (Hull 2000, Rodary *et al.* 2000, Lescroël and Bost 2005). Two broad ideas have arisen to explain diving behaviour in marine predators: 1) that animals display benthos or oceanographic feature-related diving tactics, and 2) that diving tactics are influenced primarily by prey behaviour. Examples of feature-related tactics include emperor penguins *Aptenodytes forsteri* that seek shallow areas to dive to the seafloor (Rodary *et al.* 2000), little penguins *Eudyptula minor* that benefit from foraging in waters with strong thermal stratification (Ropert-Coudert *et al.* 2009) or those that follow the seafloor of channels that are dredged for shipping (Preston *et al.* 2007). Other animals such as seals chose to dive in areas that are linked to sea surface temperature, sea level anomalies and eddies (Ream *et al.* 2005, Simmons *et al.* 2007). These compare with the prey-related tactics used by king penguins *Aptenodytes patagonicus* that dive to depths consistent with daily vertical migration of their myctophid prey (Moore *et al.* 1999).

One of the most commonly reported diving variables is dive depth, which often determines the prey type that can be accessed (Williams *et al.* 1992). The dive depth of king penguins at Heard Island varies seasonally from shallow diving in summer when they prey diurnally on myctophids, to deeper diving in winter when they prey on squid (Moore *et al.* 1999). Diving depths may also be limited by light, as penguins are visual predators, they require daylight for diving (Robinson and Hindell 1996, Ropert-Coudert *et al.* 2006).

Penguin diving capabilities, especially dive depths, tend to be correlated with body size and oxygen storage capabilities, with the depths of dives ranging from > 500 m in the largest species (emperor penguins), to < 50 m in the smallest species (little penguin) (Wilson 1995, Kooyman and Kooyman 1995, Bethge *et al.* 1997, Chiaradia *et al.* 2007). Even within a species, such as the sexually dimorphic emperor penguin, the larger males tend to dive deeper for longer durations than females (Wienecke and Robertson 1997). Diving strategies are also influenced by the energy costs associated with dive frequency, depth, speed and duration (Green *et al.* 2003). If the energy costs of diving strategies are not rewarded with sufficient food, body condition, mass and breeding success can be affected, particularly in Humboldt penguins *Spheniscus humboldti* (Hennicke and Culik 2005).

By using benthic prey, some marine predators have broadened their foraging niche beyond that of the water column (Ropert-Coudert *et al.* 2003). Benthic diving is important for several penguin species including macaroni *Eudyptes chryolophus* (Deagle *et al.* 2008), gentoo penguins *Pygoscelis papua* (Robinson and Hindell 1996) and emperor penguins (Rodary *et al.* 2000). At Penguin Island in Western Australia, little penguins are mostly benthic foragers because they spend most of the dive time and pursue most prey at a depth that is consistent with the seafloor, allowing them to trap prey against the bottom (Ropert-Coudert *et al.* 2006). Although little penguins can use both benthic and pelagic strategies, the ability to exploit benthic prey appears important at some sites where penguins fledge a high proportion of chicks (Ropert-Coudert *et al.* 2003, Chiaradia *et al.* 2007). For instance, poorer fledging success was exhibited at two colonies where deep foraging habitats coincided with greater diving effort and deeper diving by breeding adults (Chiaradia *et al.* 2007). Conversely, a seafloor that is beyond the diving capabilities of the penguin (mean dive depth 5-13 m, generally < 50 m) may allow some prey to escape downwards (Chiaradia *et al.* 2007).

Little penguins forage in close proximity to their colonies, which makes them good subjects for the investigation of how dive behaviour varies with surrounding seafloor depth. The foraging areas of little penguins at Troubridge and Pearson Islands, in South Australia are characterised by contrasting depth. Foraging areas surrounding Troubridge Island in Gulf St Vincent are typically less than 40 m deep, and are characterised by sea grass, rocky reef and sand habitats (Tanner 2005). In contrast the foraging areas surrounding Pearson Island in continental shelf waters are deeper (50 -100 m), much of which is likely to be beyond the diving range of little penguins (Chiaradia *et al.* 2007). I investigated if the diving behaviour of little penguins differed between these deep and shallow environments. I hypothesised that little penguins would dive deeper and spend more time diving in the deep environment because their prey have a greater ability to escape to deeper depths (Chiaradia *et al.* 2007). In contrast, I expected that penguins in the shallower environment would dive shallower and to the seafloor, which would reflect their ability to target prey throughout the water column and at the benthos.

Methods

The study was conducted at Troubridge Island (35°07'S, 137°50'E) in lower Gulf St Vincent, and at Pearson Island (33°57'S, 134°15'E) in the eastern Great Australian Bight of South Australia (Fig. 1 in Chapter 1) in July 2004.

Diet samples were collected from little penguins during the study period (4th -12th July 2004) at Troubridge and Pearson Islands. Adult birds were captured at random by hand on the shore as they returned from foraging trips. Stomach content samples were obtained using the stomach lavaging technique (Wilson 1984). After lavaging, penguins were fed 40 ml 10 % aqueous Vy-Trate ® and 50 g of blended (beheaded and scaled) sardine through a 6 mm diameter feeding tube (Unomedical™) (see methods in Chapter 4). Birds were then placed in a quiet, dark pen for 30 mins to ensure they were fit for release.

Diet samples were sieved through a 0.5 mm mesh and hard parts (e.g. eyes), cephalopod beaks and otoliths were removed. Variables that described diet were calculated as 1) the minimum number of prey items per meal, 2) the estimated meal mass (g), 3) mean prey length (mm), and 4) mean prey mass (g) (see methods in Chapter 4). Variables for the most common prey species (Australian anchovy *Engraulis australis*) were also calculated as mean length (mm), mean mass (g) and mean proportion (by number and biomass) found in the diets (Chapter 4).

Seafloor depth data for the waters surrounding each colony were sourced from marine bathymetric charts (1:300 000, AUS345 Gulf of St Vincent and approaches, and AUS342 Streaky to Whidbey Isles), which provided the average depth of the sea floor for each 2 x 2 km grid cell. Data from these charts were collated from oceanic areas within a 20 km radius of each colony, which encompasses the main foraging range of breeding little penguins at most sites (Collins *et al.* 1999, Wienecke *et al.* 1995, Bool *et al.* 2007).

Adult penguins tending their chicks (aged < 1 week old) were fitted with time-depth recorders (TDRs) (MK9, Wildlife Computers, Redmond, Washington) for one foraging trip. TDRs were programmed to record depth (in increments of 0.5 m), light (W.cm^{-2}) and time (1 sec intervals). TDRs were glued onto several back feathers using Loctite® and secured with a small cable tie. Birds were weighed (±5 g) and sex was determined by discriminant functions based on bill depth (*BD*) and bill length (*BL*) measurements (±0.01 mm) (Chapter 2). Body condition (mass relative to skeletal size) was calculated as mass/*BD* (where *BD* was used as proxy for skeletal size). Since the best way to retrieve TDRs was to catch birds in burrows, after they had fed their chicks, these birds were not stomach lavaged. All birds continued to breed normally following TDR removal.

Data analyses

Before analysis, depth sensor drift was corrected using Instrument Helper (beta version 9.01, Wildlife Computers, Redmond, Washington). Only dives deeper than 1 m were included in the analysis (Kato *et al.* 2008). Ten parameters that described dive behaviour were calculated: number of dives, time spent diving, total time spent foraging during the day, dive depth, dive duration and bottom time (time spent at > 90 % of the maximum depth of the dive) (Charrassin *et al.* 2002, Deagle *et al.* 2008). I also calculated the period in which each penguin foraged (first dive to last dive of a trip). Other descriptors included vertical ascent and descent time (travel duration between the surface and the depth at which bottom time commenced or terminated respectively, Deagle *et al.* 2008).

From these measurements, the following values were derived: 1) proportion of the foraging time allocated to diving, 2) proportional bottom duration (bottom time/ dive duration,Chiaradia *et al.* 2007) and 3) proportion of dives with a maximum depth > 10 % deeper or shallower than the preceding dive, which represent non-benthic diving (method modified from Deagle *et al.* 2008). The profiles of adjacent dives with maximum depths that are considerably different from each other (i.e.

dives with depths that vary by > 10 %) are unlikely to reflect the gently undulating topography of the seafloor and therefore represent non-benthic diving (Fig. 2.) To check whether 10 % variation between adjacent dives was a reasonable cut-off to indicate non-benthic diving, I compared the slope of the seafloor with the slope of adjacent dives that varied by > 10 % in depth (either side of the mean dive depth). The slope of the seafloor surrounding Troubridge and Pearson Islands (max 2 m.km^{-1} and 4 m.km^{-1} respectively, determined from bathymetric charts) is shallower than the slope between adjacent dives with depth variations of > 10 % (min 4.4 m.km^{-1}). The minimum slope between these adjacent dives was calculated using mean surface time between dives (27.3 s, TDR data) and mean travel speed (3.9 km/hr, satellite tracking data, A. Wiebkin unpublished data), which estimated that dives were, on average, 29.5 m apart.

Results are reported in means ± SD. All data were tested for homogeneity of variances before parametric analyses were used. I considered differences to be significant if $P < 0.05$ and they approached significance if $P < 0.1$.

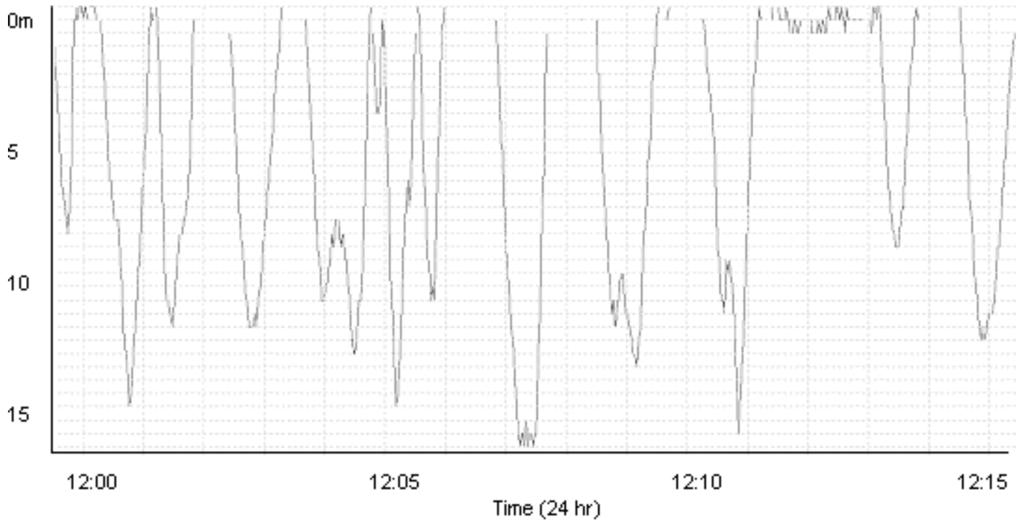

Figure 2. Example dive profiles of a little penguin from Troubridge Island, showing dive depth (m) and time (h).

Results

We collected 49 stomach lavaged diet samples from Troubridge Island and 29 from Pearson Island (data from Chapter 4, July 2004 samples only to coincide with TDR deployment). From these 1,774 and 1,339 prey items were identified, respectively. Seven species of prey were identified, which accounted for > 97 % of the prey items found. Australian anchovy *Engraulis australis* was most important prey, with a total biomass of 82 % and 92 % of total prey biomass at Troubridge and Pearson Islands respectively (Table 1). At Troubridge Island, the other prey species were sardine *Sardinops sagax* (9 % biomass), garfish *Hyporhamphus melanochir* (1 %), blue sprat *Spratelloides robustus* (7 %), slender bullseye *Parapriacanthus elongatus* (< 1 %) and Gould's squid *Nototodarus gouldi* (< 1 %). At Pearson Island, the other prey species were sardine (7 % biomass), garfish (1 %) and redbait *Emmelichthys nitidus* (< 1 %). Prey, particularly anchovy had significantly higher mean masses at Troubridge Island than those at Pearson Island (Table 1). Penguins from Pearson Island consumed significantly more individual prey (64 ± 6 vs 49 ± 5) to obtain meal masses that did not differ significantly from Troubridge Island (183 ± 16 g and 173 ± 18 g; Table 1).

Males and females from Troubridge Island were significantly larger (8.6 % and 8.9 % larger in mass and each sex was 9.4 % larger in bill depth), and when sexes were pooled they also had significantly higher mean body conditions than those from Pearson Island (89 ± 2 vs 84 ± 2; Table 1). Dietary variables and body condition did not vary significantly between sexes within colonies ($P > 0.05$ in all cases). There were also no significant correlations between penguin mass or bill size and mean fish mass or length, within colonies and for colonies combined ($P > 0.5$ in all cases). The largest prey items consumed at each colony were garfish (max. 195.6 and 173.6 mm, 15.8 g and 10.0 g, respectively). There was no significant difference in the returning body mass between instrumented and non-instrumented birds ($P > 0.1$).

Table 1. Summary table of the size and biomass of meals, prey, principal prey species (anchovy) and the bill size, body mass and condition of the penguins from which the diet samples were obtained. *** highly significant, ** significant, NS not significant.

		Troubridge Island		Pearson Island			
Variable	Sex	Mean ± SD	*n*	Mean ± SD	*n*	*t*	*P*
Penguin bill depth (mm)	*M*	15.1 ± 0.5	26	14.2 ± 0.7	11	3.5	0.002**
	F	12.9 ± 0.5	23	12.1 ± 0.9	19	4	<0.001***
Penguin mass (g)	*M*	1320 ± 112	26	1144 ± 93	11	4.6	<0.001***
	F	1167 ± 192	23	1046 ± 122	19	2.4	0.022**
Penguin body condition (mass/*BD*)		89 ± 14	49	84 ± 11	29	2	0.048**
Minimum # of items per meal		47 ± 37	49	65 ± 35	29	2.1	0.044**
Meal mass (g)		173 ± 126	49	183 ± 86	29	0.4	NS
Mean fish length (mm)		78 ± 14	49	76 ± 6	29	0.8	NS
Mean fish mass (g)		5.1 ± 2.3	49	4.3 ± 0.9	29	2	0.047**
Mean anchovy length (mm)		84 ± 9	49	80 ± 4	29	2.9	0.004**
Mean anchovy mass (g)		6.0 ± 2.1	49	4.7 ± 0.9	29	3.3	<0.001***
Percent numerical abundance of anchovy per meal (%)		72 ± 28	49	83 ± 16	29	2.2	0.030**
Biomass of anchovy per meal (%)		82 ± 21	49	92 ± 11	29	2.6	0.012**

The seafloor depth within 20 km of Troubridge Island was significantly shallower than around Pearson Island (mean 20.3 ± 11.7 m (max. 41.8 m) vs 62.8 ± 19.3 m (max. 92.0 m), $t = 16.8$, $P < 0.001$; Fig. 3.). In contrast, the mean dive depths from penguins at Troubridge and Pearson Islands were both shallow and did not differ significantly between sites (12.0 ± 2.4 m vs 13.4 ± 3.6 m, $t = 0.6$, $P > 0.05$; Fig. 3). The deepest dives at each colony were 21.5 m and 47.5 m, respectively. Pearson Island had more foraging area that was deeper than the colony's deepest dive (Pearson: 76 % vs Troubridge: 49 %) and mean dive depth (Pearson: 99 % vs Troubridge: 65 %).

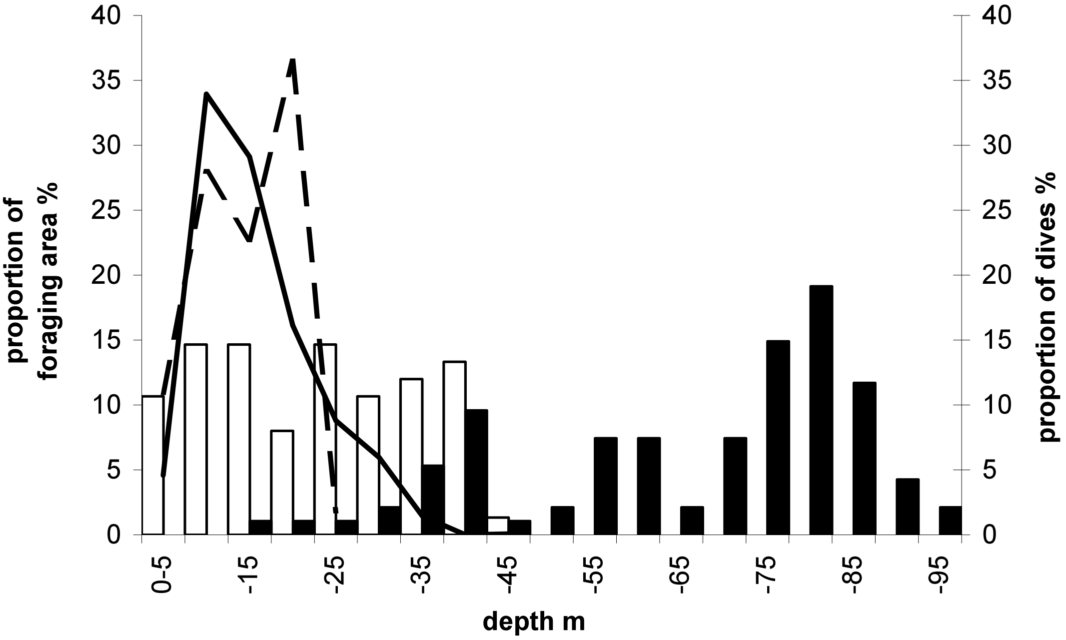

Figure 3. The proportion of foraging area (bars) at each 5m-depth interval, and the proportion of dives at each depth (lines) for little penguins at Troubridge (hollow bars and dotted line) and Pearson (solid bars and line) Islands.

Dives were recorded from nine different adults at Troubridge Island that comprised a total of 3,523 dives and 391 ± 46 dives per individual penguin, and three adults at Pearson Island that comprised a total of 1,593 dives with an average of 534 ± 52 dives per individual (Table 2). All penguins made single-day foraging trips. Penguins from Troubridge and Pearson Islands commenced diving up to a maximum of 45 and 22 mins before sunrise and ceased diving up to a maximum of 26 and 16 mins after sunset, respectively. The diving period (from the first dive of the day until the last) did not vary significantly between Troubridge and Pearson Islands (10.3 ± 0.4 h vs 10.4 ± 0.1 h, $P > 0.05$).

Table 2. Summary table of the body parameters and sex of the birds deployed with TDRs and the dive periods from which data was data was recorded.

Island	Sex	Date	*BM* g	*BD* mm	*BL* mm	Start diving time	Stop diving time	Diving period h	No. dives	% of diving period spent under water	Mean dive time ± SD s	Mean dive depth ± SD m	Max dive depth m
Troubridge	F	13/07/04	1240	12.3	30.9	06:55	17:32	10.6	343	28	32.1 ± 10.6	11.1 ± 3.8	18.3
Troubridge	M	14/07/04	1470	15.8	40.1	07:01	17:34	10.5	329	35	26.0 ± 14.8	8.6 ± 4.3	19.0
Troubridge	F	7/07/04	1220	12.8	36.6	07:07	17:31	10.4	393	27	41.4 ± 13.4	14.3 ± 4.0	18.0
Troubridge	M	8/07/04	1630	16.3	41.0	07:08	17:13	10.1	610	41	24.4 ± 12.5	7.9 ± 4.3	17.5
Troubridge	F	7/07/04	1080	12.6	37.9	07:03	17:10	10.1	276	26	35.5 ± 15.0	13.1 ± 4.2	18.5
Troubridge	F	9/07/04	1150	14.0	37.7	06:52	17:11	10.3	323	36	41.9 ± 13.3	14.5 ± 4.8	21.5
Troubridge	F	10/07/04	1160	13.6	37.8	06:51	17:46	10.9	548	60	43.4 ± 17.0	12.3 ± 4.0	20.0
Troubridge	M	10/07/04	1360	15.1	38.9	06:54	17:37	10.7	516	46	34.7 ± 13.7	12.0 ± 5.3	21.0
Troubridge	M	12/07/04	1260	15.9	42.6	07:05	16:34	9.5	185	26	48.2 ± 16.2	14.6 ± 3.1	18.0
Pearson	M	4/07/04	1050	14.0	41.6	07:20	17:41	10.4	515	50	36.3 ± 12.7	11.7 ± 4.8	47.5
Pearson	M	6/07/04	1140	14.5	39.9	07:25	17:44	10.3	455	51	43.0 ± 17.6	17.5 ± 8.0	34.5
Pearson	F	8/07/04	1120	11.8	36.2	07:22	17:50	10.5	633	66	36.6 ± 23.2	10.9 ± 5.2	31.5

Most parameters that described dive behaviour, including mean dive durations, descent times, proportion of dives with depth > 10 % deeper or shallower than the preceding dive, and bottom times were not significantly different between colonies (Table 3). This is despite differences in foraging patterns, where penguins from Pearson Island spend longer at sea and swim further on foraging trips than those from Troubridge Island (Chapter 6). Penguins from Pearson Island spent significantly more time diving (5.8 ± 0.6 h vs 3.8 ± 0.4 h) and less time on the surface (4.7 ± 0.3 h vs 6.2 ± 0.3 h; Table 3, Fig. 4). They also made a higher mean number of dives, which approached significance (Table 3). The depth and time spent diving was relatively consistent throughout the day at Troubridge Island ($r^2 = 0.40$ $P > 0.1$, mean depth 12.4 ± 1.1 m during each hour of the dive period), where as penguins at Pearson Island dived deeper during consecutive hours until mid afternoon ($r^2 = 0.85$, $P = 0.02$, mean depth 13.5 ± 13.2 m each hour of the dive period; Fig. 5). Bottom time as a proportion of the whole dive was significantly greater at Troubridge Island because ascent time was significantly shorter (Table 3). Neither penguin size (body mass, *BD* and *BL*) nor sex was significantly correlated with any dive behaviour parameter.

Table 3. Average dive behaviour variables (± SD) calculated for foraging trips at Troubridge and Pearson and the significance of differences between averages using unpaired t-tests. Troubridge *n* = 9, Pearson *n* = 3. ** *P* < 0.05 significant, * *P* < 0.1 approaching significance, NS not significant.

	Troubridge Island	Pearson Island		
	mean ± SD (*n* = 3523)	mean ± SD (*n* = 1593)	*t*	*P*
Number of dives (per day)	391.4 ± 138.9	534.0 ± 90.6	2.1	0.090*
Total diving duration (h)	3.8 ± 1.2	5.8 ± 1.0	2.8	0.042**
Total surface duration (h)	6.2 ± 0.9	4.7 ± 0.5	3.5	0.016**
Bottom time/dive duration (%)	35.2 ± 5.4	29.0 ± 2.9	2.5	0.041**
Ascent time (sec)	10.6 ± 1.8	12.7 ± 0.9	2.7	0.032**
Descent time (sec)	13.0 ± 2.4	15.7 ± 2.8	1.5	NS
Dive duration (sec)	36.4 ± 8.1	38.6 ± 4.0	0.6	NS
Dive depth (m)	12.0 ± 2.4	13.4 ± 3.6	0.6	NS
Dives with depth > 10 % deeper or shallower than preceding dive % (non-benthic dives)	57.2 ± 12.4	49.8 ± 22.3	0.5	NS
Bottom time (sec)	13.7 ± 1.6	10.9 ± 0.6	1.6	NS

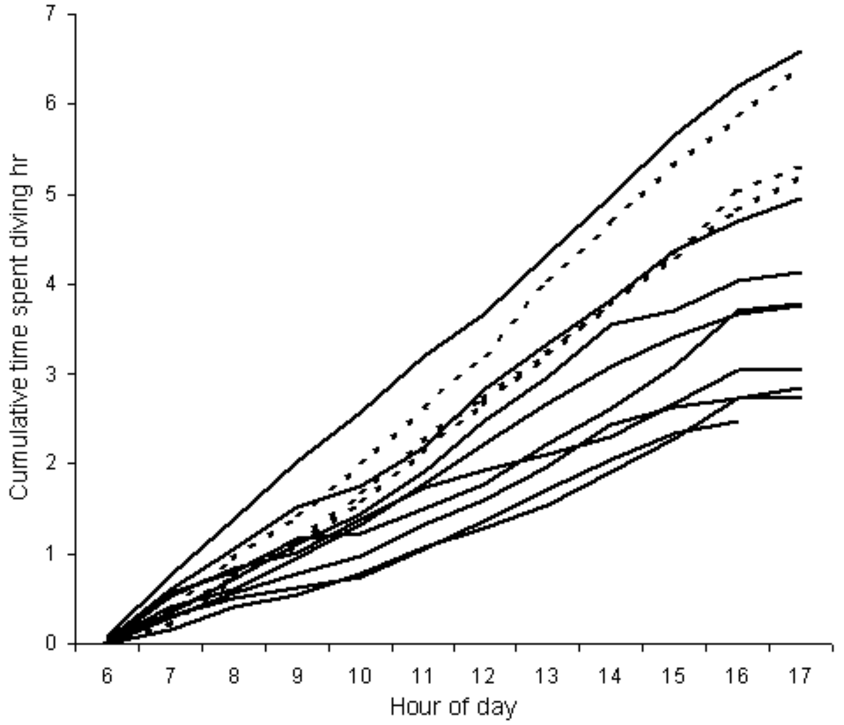

Figure 4. Cumulative time (h) spent diving during each hour of the day for individual little penguins that were fitted with TDRs, at Troubridge (solid line) and Pearson (dashed line) Islands.

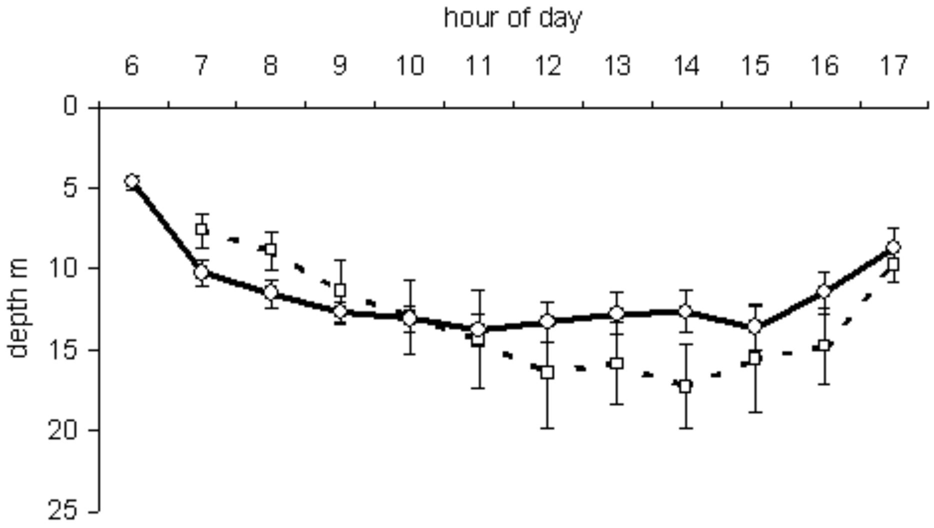

Figure 5. Average dive depths ± SE at each hour of the day at Troubridge Island (solid line and circles) and Pearson Island (dashed line and squares).

Discussion

This study shows that despite significant differences in water depths between the two sites, little penguins foraged to similar depths to catch their preferred prey, anchovies. Previous studies indicate that little penguins prey on abundant small pelagic fish or squid near their colonies (Klomp and Wooller 1988, Gales and Pemberton 1990, Chiaradia *et al.* 2003). In this study juvenile anchovies dominated the diet across the region and across different marine habitats and depths. Because penguins foraging in the pelagic realm follow the depth movements of their prey (Williams *et al.* 1992), the similar diving depth of penguins from both colonies suggests juvenile anchovies had a vertical distribution that encompassed the surface layers. Given the importance of anchovies in the diet, the foraging depths of little penguins are likely to reflect the depths at which these fish usually occur. Winter foraging (breeding season) may be optimal for little penguins if anchovies are at shallower depths than in other seasons (spring and summer) when thermoclines form.

Despite similar diet composition at both locations, the larger Troubridge Island birds caught larger anchovy, either because the local fish were larger or because larger fish were selected. In some seabird species, birds with larger bills and masses such as those of male Crozet cormorants *Phalacrocorax melanogenis*, allow them to catch and kill larger prey (Cook *et al.* 2007). Little penguins are also sexually dimorphic in bill size and one study showed that males predated on significantly larger prey items at Phillip Island (Shaw *et al.* 2007). In contrast, my data indicated that males (large bills) and females (smaller bills) consumed anchovies that did not differ significantly in size at each colony (Chapter 3 and this study). There were also no significant correlations between penguin mass or bill size and prey size. This may be because little penguins from both sites were capable of consuming much larger prey than mean prey sizes, and in Victoria, prey as long as 300 mm have been recorded (Cullen *et al.* 1992). It is likely that the differences in the sizes of anchovies caught reflect the size of available prey, rather than selectivity of prey size because penguin body and bill size did not influence the size of prey consumed.

Dive depth differs with body size where the larger males including Crozet, Antarctic *Phalacrocorax bransfieldensis*, subantarctic *P. albiventer*, Japanese *P. filamentosus* and great *P. carbo* cormorants (Casaux *et al.* 2001, Cook *et al.* 2007, Kato *et al.* 1999, Fonteneau *et al.* 2009) as well as little penguins at Penguin Island dived deeper than the smaller females (Ropert-Coudert *et al.* 2003). The size difference between little penguins from Troubridge and Pearson Islands approaches the sexual size differences in these cormorants that exhibit size related behavioural differences. Unlike these studies, the smaller size of the Pearson Island penguins did not appear to limit physiological dive capabilities (such as dive depth, duration and descent rate) but they were required to expend more energy (in time) diving to catch similar total masses of prey. Previous studies on Humboldt penguins *Spheniscus humboldti* found that increased energy expenditure on foraging resulted in poorer rates of offspring growth (mass and bill size), survival and reproductive success (Hennicke and Culik 2005). Likewise, the increased energy required to obtain sufficient food may underlie the lower body condition of Pearson Island individuals. Alternatively, consistently lower prey availability at Pearson Island may lead penguins to select prey of smaller size, which may have become an evolutionary evolved response.

Despite a requirement to expend more energy (more dives) for the same daily meal mass, the population size of breeding penguins at Pearson Island (~12,000 breeding adults) is much larger than at Troubridge Island (~3,000 breeding adults; Chapter 6) and it is the largest in South Australia (Wiebkin 2011). Foraging strategies of Pearson Island penguins must therefore be as good as or better than those at Troubridge Island. Small body size can be an adaptation to more efficient, faster foraging in an exclusively pelagic environment. This is evident in the smaller species of fur seals that forage for small, fast prey at mid-water depths compared with the larger Australian fur seals that forage for slower prey at the benthos (Arnould and Hindell 2001). The smaller sex of the highly dimorphic brown booby *Sula leucogaster* also dives 2.6 times more than the larger sex (Lewis *et al.* 2005), which at least in albatrosses, is possibly due to lower dive-costs (particularly on post-dive take-off) (Weimerskirch *et al.* 2000). Small size also benefits foraging efficiency of grey seals because when they are thin (less buoyant) they can descend to foraging depths faster than when they are fat (prior to breeding) (Beck *et al.* 2000). The slower ascent time of the smaller Pearson Island little penguins could likewise be due to reduced fat reserves (lower body condition), or less air in the feathers and respiratory systems of their smaller bodies (Kato *et al.* 2006). Further investigations into the prey searching strategies of penguins may determine whether the smaller bodied Pearson Island birds have more efficient ways of finding prey patches, although preliminary results from this study suggest that penguins from both colonies have similar rates of fishing success per dive (mean prey items/mean number of dives; both 12 %). Alternatively, the smaller size of Pearson Island penguins requires lower energy costs to hunt their prey.

The readily accessible seafloor surrounding Troubridge Island (20.3 m) provided opportunities for benthic diving yet most dives did not appear to be following the topography of the seafloor. We can assume this because Troubridge Island penguins dived to inconsistent depths during 57 % of the dives. This compares with the frequent benthic diving behaviour of other penguins, including macaroni penguins, evident in highly consistent depths of adjacent dives (84 %, Deagle *et al.* 2008). Little penguins in other locations, such as Penguin Island also predominantly dive to the shallow seafloor to depths of 5 – 13 m (Ropert-Coudert *et al.* 2003, Chiaradia *et al.* 2007), where penguins principally target sandy sprat *Hyperlophus vittatus*, southern sea garfish and blue sprat (Klomp and Wooller 1988, Gomon *et al.* 2008). At Troubridge Island, penguins probably chased prey near the benthos some of the time because 35 % of the seafloor was at depths within the mean dive depth of penguins. This near-benthic foraging niche may provide opportunities to take a more diverse array of prey, and the diet at Troubridge Island was marginally more diverse and included slender bullseye and juvenile southern sea garfish, generally associated with rocky reef and shallow seagrass meadows, respectively (Gomon *et al.* 2008). These prey, however, contributed little to the diet. Although shallow-water habitats offer the opportunity to use benthic trapping of prey against the seafloor, this study indicates that little penguins at Troubridge and Pearson Islands primarily employed pelagic diving strategies to catch prey.

Differences in diet and diving behaviour of little penguins across their range support the theory that they use prey-specific foraging tactics that reflect prey type, behaviour and distribution in the water column, rather than benthos-related foraging tactics. At Phillip Island, where penguins forage in deeper water (Chiaradia *et al.* 2007), they target sardine, barracouta *Thyrsites atun* and Gould's squid (Cullen *et al.* 1992), which are pelagic species. Gentoo penguins follow the vertical diel movements of krill, which are their main prey at some sites (Williams *et al.* 1992). Similarly, the little penguins at Pearson Island dived increasingly deeper until mid afternoon presumably following the movement of the anchovies. While many studies illustrate the relationship between prey and diving strategies, few compare sites that provide the same prey but differ in habitat. My study supports this relationship and shows that little penguins dive to similar depths when targeting the same prey, even when the habitat bathymetry is very different.

Little penguin colonies breed at different times of the year, which most likely reflects the season when local food availability is greatest or when day length is longest for prolonged foraging (i.e. summer). Most other penguin species breed in the high latitudes, where day length varies considerably between summer and winter, and these penguins have relatively tight chick-rearing periods in the summer when day length is greatest, (Davis *et al.* 2001, Green *et al.* 2007). Similarly the breeding season at most little penguin colonies in Victoria, New Zealand and Tasmania breed in spring and summer (Gales and Pemberton 1990, Dann *et al.* 2000, Miyazaki and Waas 2003) when the day length is either increasing and/or longest (e.g. Chiaradia *et* *al.*2007). Because the day length is briefer in winter, the penguins in South Australia have up to 33 % less daytime in which to forage. For this reason, dive numbers per day at Troubridge and Pearson Islands were lower than those from Phillip Island (391-534/day vs 585-775/day Kato *et al.* 2008). King penguins also provision chicks during winter (Moore *et al.* 2007), but they have specialised eyes for foraging at depth (Martin 1999). Little penguins are, however, reliant on good visibility, and even turbidity can reduce diving performance (Ropert-Coudert *et al.* 2006). My data, which shows that penguins from Troubridge and Pearson Islands can catch sufficient food for breeding during winter, with less total dive duration than those from other regions, suggests that prey availability and/or foraging success during the winter (particularly Troubridge Island, Chapter 3), is higher than at other colonies. In South Australia, the limitation of reduced day length in the winter breeding season does not seem to affect the prey that can be caught.

Little penguin colonies have a coastal distribution but an accessible seafloor depth does not dictate their distribution across the region because little penguins can adapt their foraging behaviour to target pelagic or benthic prey. Evidence supports the hypothesis that access to shallow habitats influences fledging success (Chiaradia *et al.* 2007) and that shallow habitats allow penguins to spend less time (and energy) diving (this study). However, a deep seafloor depth does not appear to affect population sizes, particularly those populations that are large at Pearson Island and Phillip Island (Chiaradia *et al.* 2007). This study suggest that other than the distribution of suitable breeding islands, the spatial distribution and availability of juvenile anchovies are likely to be the most significant factors determining the distribution and size of penguin colonies in South Australia.

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Chapter 6: Why are some little penguins so little: an effect of Ashmole's halo on foraging behaviour?

Abstract

Little penguins *Eudyptula minor* were satellite tracked at four colonies in the eastern Great Australian Bight to investigate variation in foraging behaviour. Breeding penguins from three coastal sites foraged to mean maximum distances of 13 - 21 km from their colonies, and they swam total distances of 49 - 102 km during mostly one-day trips. These distances differed significantly from those travelled by breeding penguins from the largest colony, which was also the furthest from the mainland. The penguins from this large colony swam up to three times as far, with mean maximum distances of 39 km, and for three times the duration (3 days), which meant that parents fed their chicks less frequently. A likely reason that penguins foraged further afield was that their prey was less profitable to catch near the colony (through depletion or less dense patches of prey) a phenomenon known as Ashmole's halo. At the coastal colony penguins foraged closer to their colony and were larger than penguins from the offshore colony. The difference in body size is likely to reflect chick growth rates, which are dependent on how much and how frequently their parents feed chicks. Provisioning rates depend on the time parents spend foraging each trip. Therefore, Ashmole's halo, which forces parents to forage further away, for longer, may influence the body size of little penguins. We do not know the exact factors causing prey population densities and distributions around islands, but it is likely that Ashmole's halo contributes towards regulating the population size of large penguin colonies as well as keeping little penguins little through limited food resources at these sites. Sea-surface temperature, chlorophyll-a, water depth, seafloor slope and distance from the colony were also investigated as potential factors that might explain some of the variation in foraging behaviour of little penguins, because prey aggregate near such oceanographic and physical features. Weak relationships indicated that penguins spent more time foraging in areas of higher chlorophyll-a at one colony, in area of low chlorophyll-a at another and in areas of cooler sea surface temperatures (near-shore) at another. This indicates that local marine environments can also influence foraging behaviour in different ways.

Key words: little penguin, *Eudyptula minor*, foraging, Ashmole's halo

Introduction

Central place foragers such as seabirds are restricted to foraging near the breeding site to provision their young frequently (Orians and Pearson 1979). Because of this, large colonies of breeding seabirds have been shown to deplete food stocks close to the colony (Birt *et al.* 1987), a phenomenon known as Ashmole's halo (Ashmole 1963). This halo of depleted food may require that breeding birds from large colonies forage further afield and for longer durations compared with breeding birds from small colonies (Birt *et al.* 1987, Lewis *et al.* 2001). Such behaviour can reduce the frequency of meals offered to young and therefore impact on their growth and survival (Davoren and Montevecchi 2003). This hypothesis has been supported by studies near the Arctic, where large colonies of seabirds had lower chick growth rates and fledging masses than those from smaller colonies (Gaston et al 1983, Hunt *et al.* 1986). This suggests that there is a trade-off between the population size of the colony, the foraging effort that can be made by many individuals near the colony and the size of young.

Seabirds typically breed in large colonies where the benefits of more social interaction, enhanced mate-choice and the safety in numbers may come at the cost of chick growth or condition. Such costs have been demonstrated in the growth and fledging size of seabirds, particularly when prey availability is relatively poor (Cooch *et al.* 1991). For example, amongst lesser snow geese *Anser caerulescens caerulescens*, the mean growth rates of goslings and the mean body size of adults decreased over a 20-year period, during which time the population increased five-fold (Cooch *et al.* 1991). These reductions were attributed to reduced availability of local food resources (Cooch *et al.* 1991). Similarly, crested terns *Thalasseus bergii* that were hatched in years when sardine stocks were particularly low grew to be smaller adults than those that hatched in years of normal prey abundance (McLeay et al. 2009). In contrast, smaller colonies that exhibit less intraspecific competition can give rise to relatively large adults in fairy martins *Petrochelidon ariel* (Santema *et al.* 2009), higher chick growth rates in thick-billed murres *Uria lomvia* (Falk *et al.* 2002) and chicks in better condition in common murres *Uria aalge* (Davoren and Montevecchi 2003). Some species such as the magellanic penguin *Spheniscus magellanicus,* which has a skewed distribution towards higher numbers of small colonies, may also benefit from the adoption of growth strategies where young are provided with more resources (Tella *et al.* 2001).

In seabirds, the foraging patterns of adults may also impact the size of chicks at fledging, and there is also often a relationship between size at fledging and adult body size. This then may explain why there is an apparent negative relationship between body size of populations of seabirds and the distance to foraging grounds, as well as the duration of their foraging trips (Waugh *et al.* 2000, Watanuki *et al.* 2004, Hennicke and Culik 2005). For example, some albatrosses that forage far from the colony and for long periods are smaller than individuals from colonies where food is available nearby (Waugh and Weimerskirch 2003).

Little penguins *Eudyptula minor* in the eastern Great Australian Bight (GAB) offer a unique opportunity to investigate the factors that influence their foraging behaviour. Because little penguins forage close to their colonies (≤ 20 km, Collins *et al.* 1999, Bool *et al.* 2007, Preston *et al.* 2007, Hoskins *et al.* 2008) and because most seabirds in this region breed in summer, in contrast to little penguins that breed in winter, the behaviour of little penguins is less likely to be affected by competition from other colonies or species. Furthermore, the diet of little penguins is broadly similar across colonies within the eastern GAB region (> 67 % by biomass consists of juvenile Australian anchovy *Engraulis australis*, Chapter 4). Because colony sizes are very different, differences in the foraging behaviour of little penguins across colonies are likely to reflect differences in the availability and abundance of their principal prey species.

The aims of this study were to examine inter-colony variation in the foraging behaviour of little penguins, and the extent to which such differences (if present) were consistent with the Ashmole's halo hypothesis, or alternately, more influenced by variation in physical oceanographic conditions. If inter-colony differences in foraging reflected the Ashmole's halo hypothesis, I expected there would be a negative relationship between penguin body size and colony size; and between body size and distance to foraging areas. Alternately, if inter-colony differences in foraging behaviour were strongly governed by variation in physical oceanographic conditions or bathymetry as is the case for some seals (Ream et al. 2005, Simmons et al. 2007) and penguins (Rodary et al. 2000, Preston et al. 2007, Ropert-Coudert et al. 2009), then I expected colony and penguin size to be correlated to bathymetric or oceanographic variables such as depth, seafloor slope, sea-surface temperature or chlorophyll-*a*.

Methods

Study sites

The study was conducted at four little penguin colonies in South Australia, all located on offshore islands: Troubridge Island (35° 07'S, 137° 50'E), Reevesby Island (34° 32'S, 136° 17'E), Pearson Island (33° 57'S, 134°15'E) and Olive Island (32° 43'S, 133° 58'E). Troubridge and Reevesby Islands are located in relatively shallow Gulf St Vincent and Spencer Gulf < 15 km from mainland Australia; whereas Olive and Pearson Islands are located off the western Eyre Peninsula in continental shelf waters 8 and 65 km from the mainland coast, respectively (Fig. 1 in Chapter 1). The study was conducted in the winter (July-August) breeding seasons of 2004 and 2005 at Pearson Island, 2004, 2005 and 2006 at Troubridge Island, 2004 at Reevesby Island and 2006 at Olive Island.

Animal capture and transmitter deployment

The foraging behaviour of little penguins rearing chicks during the guard phase, was examined using platform terminal transmitters (PTTs) (Cricket Kiwisat 202, Sirtrack, Havlock North, NZ) (30 - 32 g), embedded in black epoxy resin and hydrodynamically shaped to reduce drag. Transmitters weighed 2.5 % of the average mass of a little penguin (1260 g), and were glued onto feathers (using Loctite® 401), positioned along the midline of the back according to the methods of Healy *et al.* (2004), and then transmitters were secured under the bed of glued feathers with a small black cable tie. I intended to deploy the transmitters on little penguins (*n* = 78) for only one foraging trip but some individuals (*n* = 4) made more than one foraging trip before they were recaptured. In these cases only the first foraging trip was used to be consistent with the other deployments. To ensure that individuals were not fitted with a transmitter twice, I subcutaneously implanted TIRIS™ (Texas, USA) Radio Frequency Identification (RFID) microchips when the penguins were recaptured. Little penguins were sexed using discriminant equations based on bill depth and length measurements (Chapter 2).

Data analyses

Satellite location data were obtained through Service Argos Incorporated (Toulouse, France). Satellite location data have a relative accuracy class for each location (ordered from most to least accurate: 3, 2, 1, A, B, Z). I determined the specific accuracy of these classes in the study region by using data from a stationary transmitter operating from a known location (near Pearson Island) for 24 days in the winter of 2004 (method modified from Vincent *et al.* 2002). To investigate foraging behaviour of little penguins fitted with transmitters, I only used the most accurate location data classes (3-A) and filtered these data using a maximum travel speed approach (McConnell *et al.* 1992). The filtering process used the R statistical software V. 2.7.0 (R Development Core Team, R Foundation for Statistical Computing, Vienna) and the 'trip' package V. 1.1-5 (M. Sumner, University of Tasmania, Hobart).

To estimate the maximum travel speed of little penguins, I used transmitter data with accuracy classes of 2 or 3 from little penguins at Pearson, Reevesby and Troubridge Islands in 2004. Initially, the straight-line distances between pairs of consecutive locations were calculated, then the accuracy errors for respective classes (calculated as per above) were added to either end of these track-fragments. For example, a track-fragment formed by a Class 3 location (with accuracy error of 0.1 km) and a Class 2 location (with accuracy error of 0.2 km), each 1 km apart, would have a minimum distance of 0.7 km and maximum distance of 1.3 km. The maximum constant speed calculated from these maximum distances was used to estimate maximum travel speeds.

After filtering the little penguin tracks, I used the 'trip' package to estimate the time that each penguin spent in a given area. 'Trip' was programmed to provide track location points along each track between the original transmitter data locations, at 1-minute (time) intervals, assuming constant swim speed between locations. 'Trip' then overlaid a grid of predetermined cell dimensions (1 x 1 km) onto the 1-minute track locations. The number of these track locations in each cell was summed. These values were assigned to a central node of each cell and equalled the amount of time (in minutes) that the little penguin spent in each cell. Time was standardised to the proportional time spent in the area (TIA) over the duration of the foraging trip. The 1-minute track locations and TIA were used to calculate the following foraging behaviour parameters for each foraging trip: (1) trip duration (h), (2) minimum total trip distance travelled (km), (3) maximum and (4) mean distance in a straight-line from the colony (km), (5) mean travel speed (km.hr^{-1}), (6) median bearing (°), (7) number of cells entered and (8) sinuosity index (ratio of total distance travelled to maximum distance from the colony). Also, variables associated with the seafloor were calculated, including (9) mean water depth (m) and (10) mean seafloor slope (m.km^{-1}) of each foraging trip. Incomplete foraging trips were excluded from analyses of trip duration, sinuosity and total and maximum distance. These foraging behaviour parameters were then compared between individuals, colonies and years to investigate temporal and spatial variation.

Little penguins typically embark on foraging trips just before dawn and return just after sunset. Successful transmissions from transmitters fitted to little penguins were not always frequent enough to determine the time at which little penguins commenced and ended foraging trips. For such cases, I estimated a mean time, relative to dawn and dusk at which all trips commenced and ended from each colony. These times could then be applied to all transmitter data where commencement and end trip times were not evident. I used data from seawater-activated time-depth recorders (TDRs) deployed on little penguins (not fitted with transmitters) at Pearson (4 trips) and Troubridge (11 trips) Islands in winter 2004 (data used in Chapter 5). TDRs recorded when penguins entered and left the sea, relative to sunrise and sunset. This allowed the 'trip period' (time spent at sea) to be estimated. I also used data from the TDRs to estimate the 'diving period' (when penguins actively foraged, relative to sunrise and sunset) of little penguins fitted with transmitters. Sunrise and sunset times for the various localities and dates were obtained using Sol-Solar Energy Calculator V.1.07 (nick@anotherurl.com, USA).

To identify the broad foraging areas and hotspots that were used by all little penguins at a colony, I analysed the 1-minute track location data using Density

Kernel in ArcView® GIS V.3.2 (Environmental Systems Research Institute, Inc., USA). Only data within the diving periods were analysed. To standardise the number of locations from individual penguins at a given colony, I used equal numbers of randomly chosen locations from each foraging trip at each colony in each year. Each kernel represented a given probability of penguin foraging activity at a given location. Kernel density probabilities of 5-95 % (in 5 % increments) were calculated using auto-calculation of grid extents and H smoothing *adhoc* values of 0.005799 for Troubridge Island in 2004, 0.005710 in 2005 and 0.006252 in 2006, 0.031954 for Pearson Island in 2004 and 0.02105 in 2005, 0.008725 for Olive Island and 0.006252 for Reevesby Island. The spatial boundaries of each kernel were interpolated in MapInfo® program V.8 (Mapinfo Corporation, Troy, USA) using Vertical Mapper® V.2 (Northwood Geoscience Ltd, USA).

Foraging area fidelity

The tracking of little penguins at Pearson and Troubridge Islands over two and three years, respectively, enabled temporal comparisons of their distribution and frequency of visitations to foraging areas. I used niche overlap analyses (modified from Schoener 1968) on the data from the kernel density analyses to estimate the degree of spatial overlap in foraging areas of all penguins fitted with transmitters (combined) between years. Grid cells of 1 x 1 km were overlaid on these data and each cell was assigned the mean probability value of all points within its borders. The following equation was used to calculate niche overlap indices of foraging behaviour between any two years at each colony:

$$O = 1 - 0.5 \times \sum_{j=1}^{n} \left| p_{1j} - p_{2j} \right|$$

where p_{1j} and p_{2j} are the standardised mean kernel density values of penguin foraging in the jth cell in each year (Troubridge: 2004, 2005, 2006; Pearson Island: 2004, 2005). The overlap (O) equals 1 if the kernel density values in each cell were the same, and equals 0 if penguins spent their time in different cells.

Colony comparisons

Similarities in foraging parameters between colonies were investigated with nonparametric analysis of similarity (ANOSIM, hierarchical cluster analysis) with a

Bray-Curtis similarity matrix, in PRIMER® V.6.1.12, (Primer-E Ltd., Plymouth, U.K.) using the means derived from maximum distance, total distance, mean distance, number of 1 km^2 cells entered and sinuosity index data at each colony (α set at ≤ 0.05). ANOSIM tests hypotheses by generating a probability value and a test statistic (*R*), which is between 1 and –1. High *R*-values (positive) indicate more variation among groups than within groups, and low *R*-values (negative) indicate more variation within groups than among groups. *R*-values that equal zero represent the hypothesis of no significant difference between groups. Similarity Percentages analysis (SIMPER, Plymouth Routines in Multivariate Ecological Research) was used to determine the differences in the contributions of foraging variables to colony foraging behaviour. I also calculated mean distance from the colony at each stage of the foraging trip in 10 % increments of trip time, to determine whether penguins travelled relatively quickly or "commuted" to and from distant foraging areas, or whether travel speed was similar throughout trips.

Population, body size and foraging correlations

Correlations between mean parameters of foraging, breeding and morphology, and population sizes were investigated using SPSS V.12.0.1 (Apache Software Foundation, U.S.) to determine whether the foraging behaviour, breeding biology and morphology of little penguins from different sized colonies supported the Ashmole's halo hypothesis. For these analyses the breeding success of little penguins was the number of chicks fledged per breeding pair. Fledglings were weighed within a week of fledging. Populations were estimated from active nest counts in the breeding seasons. Total counts of nests were made at Troubridge, Granite, West and Olive Islands. Nests were sub sampled and extrapolated at Reevesby and Pearson Islands.

Effect of environmental variables on foraging

The relationships between the proportional time spent in an area (TIA) (calculated by 'Trip") and the relevant environmental variables were analysed with MapInfo and Vertical Mapper®. The environmental characteristics were (1) mean water depth (m) interpolated from 1 x 1 km depth readings (GeoScience, Australia), (2) mean bathymetric slope (change in depth (m) for each horizontal km), (3) night-time sea-surface temperature (SST) (http://poet.jpl.nasa.gov) and (4) marine fluorescence from chlorophyll-*a* (mg.m^{-3}) (chl-*a*) indicating plant productivity (data recorded at midday, Ocean Biology Processing Group at NASA Goddard Space Flight Centre, http://oceancolor.gsfc.nasa.gov). Daily SST and chl-*a* were used where available, however, cloud cover on many tracking days prevented successful satellite sensing. Where daily data were unavailable, I used MODIS-derived weekly average data, either centred on the median day of foraging otherwise the nearest week where data were available. I also calculated anomalies for SST and chl-*a* (SST or chl-*a* values minus the TIA-weighted mean). Additionally, I calculated the distance of each cell from the colony (km).

At each colony, general linear mixed models (GLMM), analysed using R V.2.11.1 (The R Foundation for Statistical Computing) were used to fit a suite of models to the foraging (TIA) data. Individuals were treated as a random effect to account for variation in foraging among individuals, and year was a factor at Troubridge Island and Pearson Island colonies. For all colonies, GLMMs with Gaussian errors with appropriate identity link functions were used to model TIA with environmental variables. I applied a log-log transformation to TIA because the data were skewed at all colonies. Models with lower Akaike information criteria (AIC) values were considered better fitting. To ensure there was no correlation between variables, only data from diving periods were used, which generally omitted the first and last 0.6-3 hours of each trip (when animals were close to the colony) as well as overnight periods (when they were not actively fishing). Because general linear modelling assumes that variables do not share strong co-linearity, all variables within each colony were tested for correlation using SPSS V.12.0.1 (Apache Software Foundation, US). Those variables that were strongly correlated ($r^2 > 0.5$ or < -0.5, $P < 0.001$ in all cases) were used in separate models.

All data were checked for assumptions of normality and homoscedasticity using Komolgorov-Smirnov/Shapiro-Wilks' tests and Levene's test. Average values are presented with ± S.D. or ± S.E (in one case, as specified).

Results

PTT satellite transmitters were deployed on 16 female and 27 male little penguins from Troubridge Island (2004-2006), 9 and 9 from Pearson Island (2004-2005), 6 and 6 from Olive Island (2006) and 2 and 3 from Reevesby Island (2004). A full summary of foraging variables for each individual fitted with a transmitter is presented in Appendix 1.

Foraging 'trip periods' commenced at 3.15 ± 0.25 h before sunrise and ended at 1.53 ± 0.27 h after sunset at Troubridge Island, respectively; and 1.40 ± 0.35 h before sunrise and 3.11 ±0.46 h after sunset at Reevesby Island, respectively. At Pearson and Olive Island, 'trip periods' commenced and ended at 1.33 ± 0.27 h before sunrise and 0.67 ± 0.23 h after sunset, respectively. 'Diving periods' did not vary between colonies, so data were pooled and calculations were used for all colonies: they commenced at 0.30 ± 0.12 h before sunrise and ended 0.06 ± 0.01 h after sunset.

Class-specific accuracy errors were calculated from 268 location recordings from the stationary transmitter at a known location (Table 1). I used 37 track-fragments (mean 1.12 ± 0.81 h in duration) to estimate the maximum travel speed, which was 8.02 km.hr^{-1}.

Table 1. Mean accuracy error (km) ± S.D. of each class of location determined from 24 days of data collected by a PTT in a known location.

Class	*n*	mean accuracy (km)
3	137	0.20 ± 0.40
2	49	0.27 ± 0.22
1	30	0.89 ± 0.87
0	5	1.56 ± 1.40
A	23	1.39 ± 2.94
B	23	2.10 ± 2.90

Foraging behaviour

Troubridge Island

The penguins from Troubridge Island generally foraged towards the north and northeast of the colony in all three years, as well as towards the south of the colony in 2005 (Fig. 2). On average, penguins foraged for less than one day (15.9 h) in shallow areas (7-15 m) near the colony (7 km on average, 12.6 km max.; Table 2). Significant correlations between foraging variables included the following: when penguins swam faster, they reached greater maximum distances from the colony, and they entered more 1 x 1 km cells ($r^2 = 0.3$ and 0.5, $P < 0.001$). The number of cells that penguins entered also increased with foraging trip duration and maximum distance from the colony ($r^2 = 0.3$ and 0.5, $P < 0.001$). Maximum distance from the colony also increased with total trip distance ($r^2 = 0.5$, $P < 0.001$).

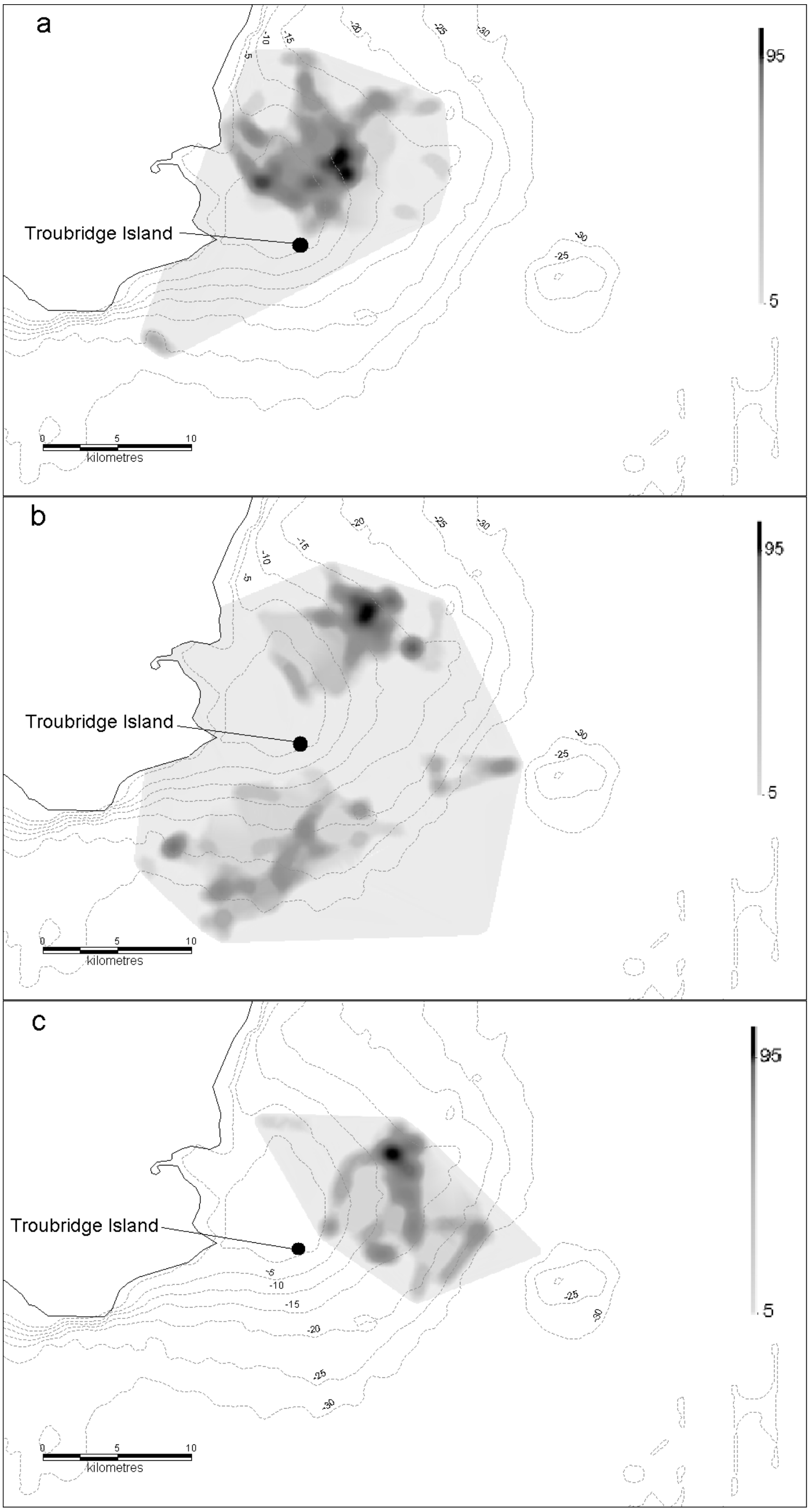

Figure 2. Kernel density plots of little penguin foraging time, (from 5-95% time, shown in legend) at Troubridge Island in the winter breeding seasons of (a) 2004, (b) 2005 and (c) 2006. Bathymetric contours are in 5 m depth increments.

Pearson Island

Penguins from Pearson Island foraged eastward in 2004 and 2005 (mean median bearings of 116.1 ± 30.6 ° and 105.6 ± 16.6 ° respectively) (Fig. 3). Penguins embarked on long trips (3 days, 150 km round trip) and foraged in deep-water areas (68 m deep) that were distant from the colony (23 km on average, 39 km max.; Table 2). Significant correlations between foraging variables included the following: the number of cells entered increased with foraging trip duration, mean maximum distance and total trip distance (r^2 = 0.9, 0.7 and 0.9, all *P's* < 0.001 respectively). Foraging trips of longer duration, and greater maximum and total distance were also significantly correlated with each other ($r^2 > 0.7$, $P < 0.01$ in all cases). An increase in most foraging parameters, including the number of cells entered, total and maximum distance, trip duration and the sinuosity of foraging tracks, were negatively correlated with body mass at the end of a trip and/or body condition gain ($r^2 < 0.3$, $P < 0.048$ in all cases).

Based on satellite telemetry data, one penguin was taken by a white-bellied sea eagle *Haliaeetus leucogaster*, approximately 72 km from Pearson Island, and carried a further 10 km to an island where the eagle nested. The satellite transmitter attached to another penguin failed within 2 hours at sea, 6 km from the colony.

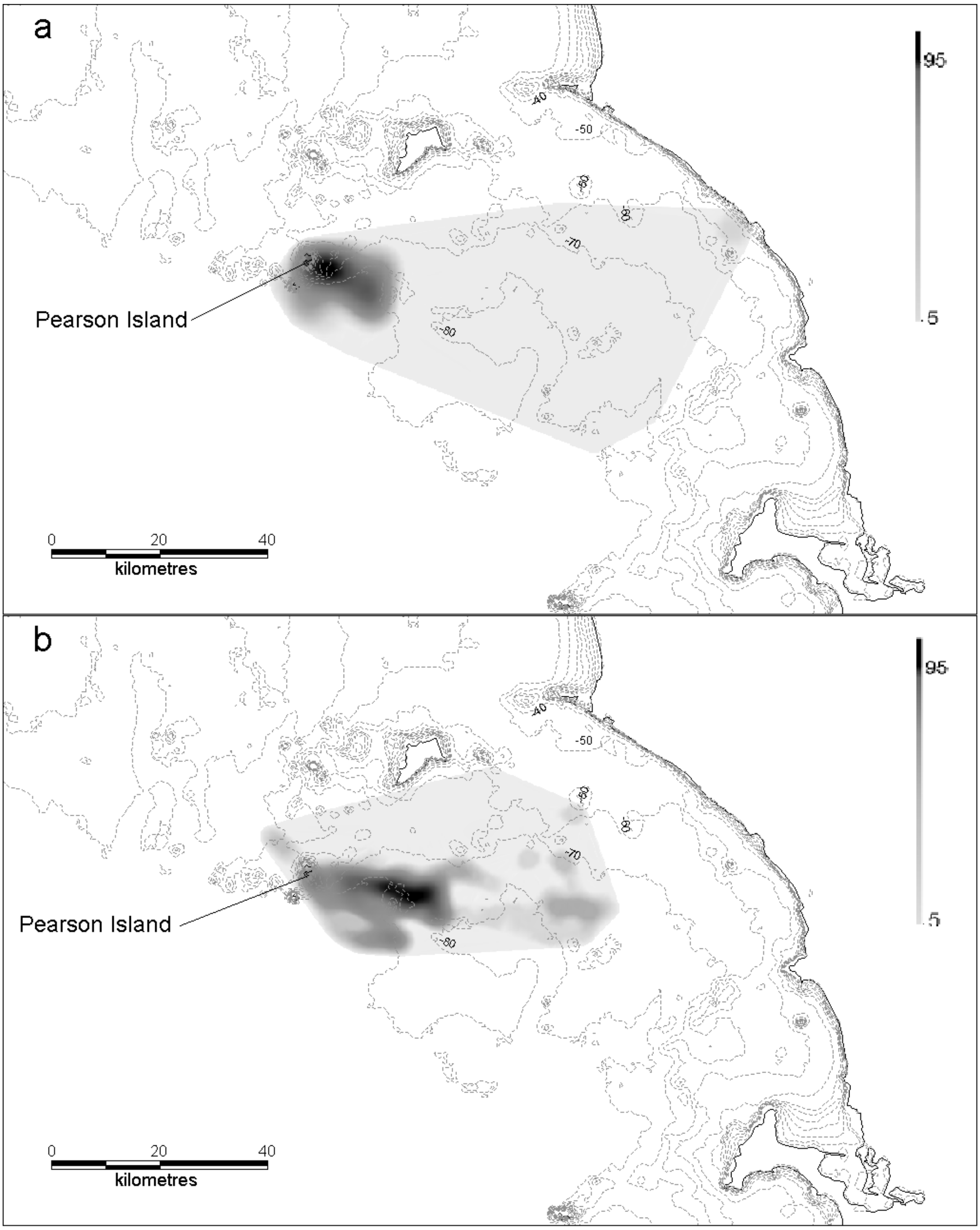

Figure 3. Kernel density plots of little penguin foraging time (from 5-95% time, shown in legend) at Pearson Island in the winter breeding seasons of (a) 2004 and (b) 2005. Bathymetric contours are in 10 m depth increments.

Olive Island

The penguins from Olive Island mostly foraged east and south of their colony (mean median bearing 140.4 ± 33.5 °) over a sloping seafloor (0.4 $m.km^{-1}$) in areas of relatively deep water (37 m mean depth) near the colony (8 km on average, 15 km max.; Fig. 4, Table 2). The area of highest foraging intensity was a hotspot near Cape Bauer (Fig. 4). Significant correlations between foraging variables included the following: mean foraging distances increased with total and maximum distance, number of cells entered and sinuosity of the track ($r^2 > 0.6$, $P < 0.004$, in all cases). Penguin body mass was positively correlated with maximum foraging distance and negatively correlated with depth ($r^2 = 0.5$ and 0.6, $P < 0.018$; Fig. 4). Foraging trip arrival mass (relative to departure mass) was positively correlated with maximum foraging distance $r^2 = 0.5$, $P = 0.024$).

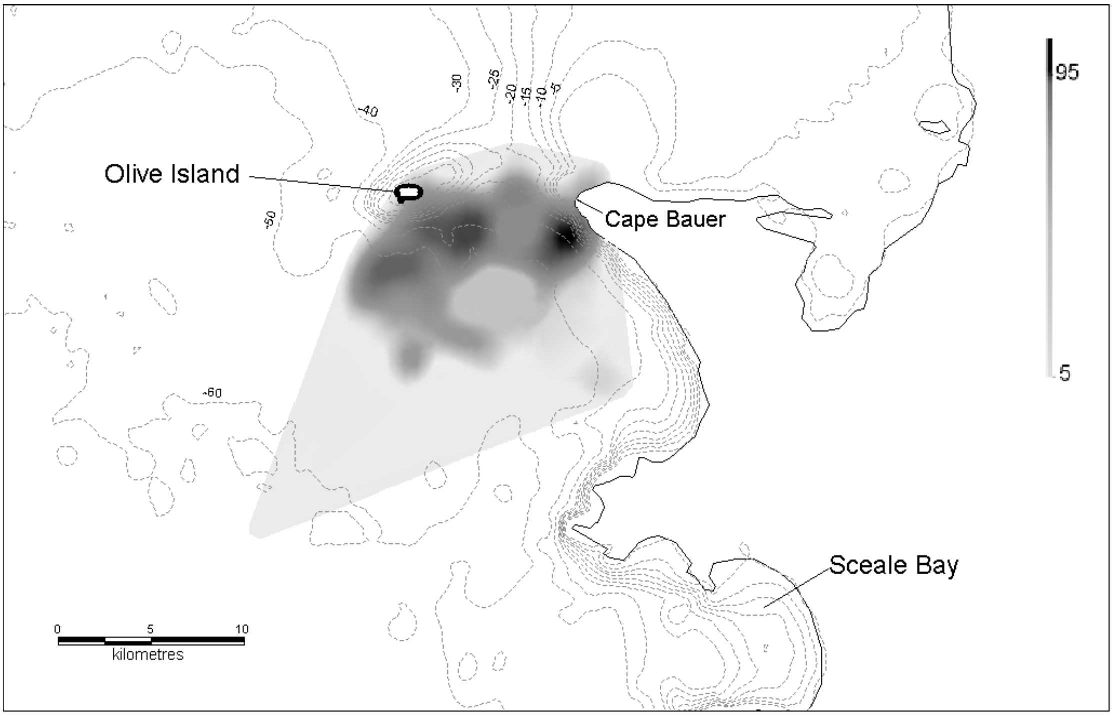

Figure 4. Kernel density plots of little penguin foraging time (from 5-95% time, shown in legend) at Olive Island in the winter breeding seasons of 2006. Bathymetric contours are in 5m depth increments.

Reevesby Island

Reevesby Island penguins foraged east and northeast of the colony (median bearing 63.8 ± 12.5°) away from nearby islands and the mainland coast in shallow water (15 m deep; Fig. 5, Table 2). Significant correlations between foraging and body variables included the following: track sinuousity was negatively correlated with body mass ($r^2 = 0.8$, $P = 0.049$), and water depth was positively correlated with arrival body mass ($r^2 = 0.8$, $P = 0.035$).

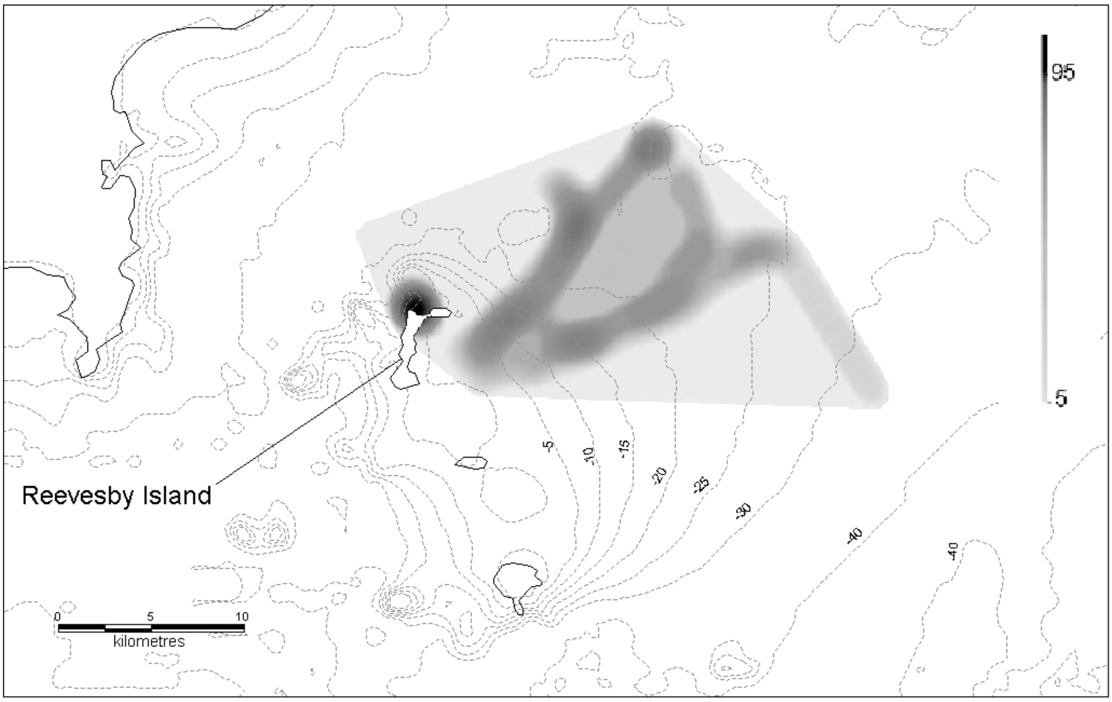

Figure 5. Kernel density plots of little penguin foraging time (from 5-95% time, shown in legend) at Reevesby Island in the winter breeding seasons of 2004. Bathymetric contours are in 5m depth increments.

Table 2. Summary table of foraging variables at each colony. ^ indicates significant differences in speed between diving and non-diving periods ($P < 0.05$).

Variables	Troubridge Island	Pearson Island	Olive Island	Reevesby Island
Mean foraging distance from colony (km)	7.0 ± 2.0*	22.9 ± 17.0	8.2 ± 5.1	10.7 ± 3.5
Mean trip duration (h)	15.9 ± 7.4	64.4 ± 84.9	16.0 ± 9.3	13.1 ± 1.3 h
Mean maximum distance from colony (km)	13.0 ± 4.5	39.2 ± 27.3	16.8 ± 13.0	21.3 ± 5.2
Mean total distance (km)	49.4 ± 17.2	170.7 ± 180.3	102.3 ± 191.3	64.4 ± 15.6
Slope of seafloor (m.km^{-1})	0.1 ± 0.01	0.4 ± 0.2	0.4 ± 0.3	0.1 ± 0.1
Mean sinuosity index (ratio of total distance to maximum distance from the colony)	3.2 ± 0.9	3.4 ± 1.5	3.9 ± 3.1	2.7 ± 0.7
Mean number of 1km^2 cells visited	44.5 ± 16.6	141.8 ± 144.5	80.1 ± 121.0	66.2 ± 14.4
Travel speed during diving period (km.h^{-1})	3.0 ± 1.0	4.5 ± 1.2	3.4 ± 0.9 ^	4.7 ± 1.5^
Travel speed during non-diving period (km.h^{-1})	3.3 ± 1.6	4.6 ± 2.4	3.9 ± 1.9^	7.3 ± 0.6^
Mean water depth (m)	14.3 ± 6.9 (m) 7.0 ± 4.8 (f)	68.4 ± 7.7	37.0 ± 10.2	14.8 ± 5.3
Total number cells entered by all tracked penguins	343 (2004) (*n*=24) 455 (2005) (*n*=15) 131 (2006) (*n*=4)	1301 (2004) (*n*=11) 696 (2005) (*n*=7)	659 (*n*=12)	223 (*n*=5)

Comparisons in colony foraging behaviour

Little penguins from Pearson Island foraged (on average) for three times as many days as those at the other colonies. Hierarchical cluster analysis indicated that the foraging behaviour parameters (max. distance, total distance, mean distance, number of cells entered and sinuosity) of penguins from Pearson Island were significantly different from those of the other three colonies, which were not different from each other (Fig. 6). Foraging variables between Pearson Island and the other colonies were 32-54% dissimilar, mostly due to differences in total distance travelled and the number of cells entered on foraging trips, which contributed up to 45.5% and 43.1% to the dissimilarity, respectively (as determined by SIMPER). Behavioural differences were significant because Pearson Island penguins foraged 1.9 – 3.0 times further away from the colony on trips that were 1.7 - 3.5 times greater in total distance, 2.8 - 3.2 times greater in mean distance, and over water that was 1.9 - 7.0 times deeper than those from all other colonies ($F > 3.3$, LSD *post hoc* tests, $P < 0.023$ in all cases).

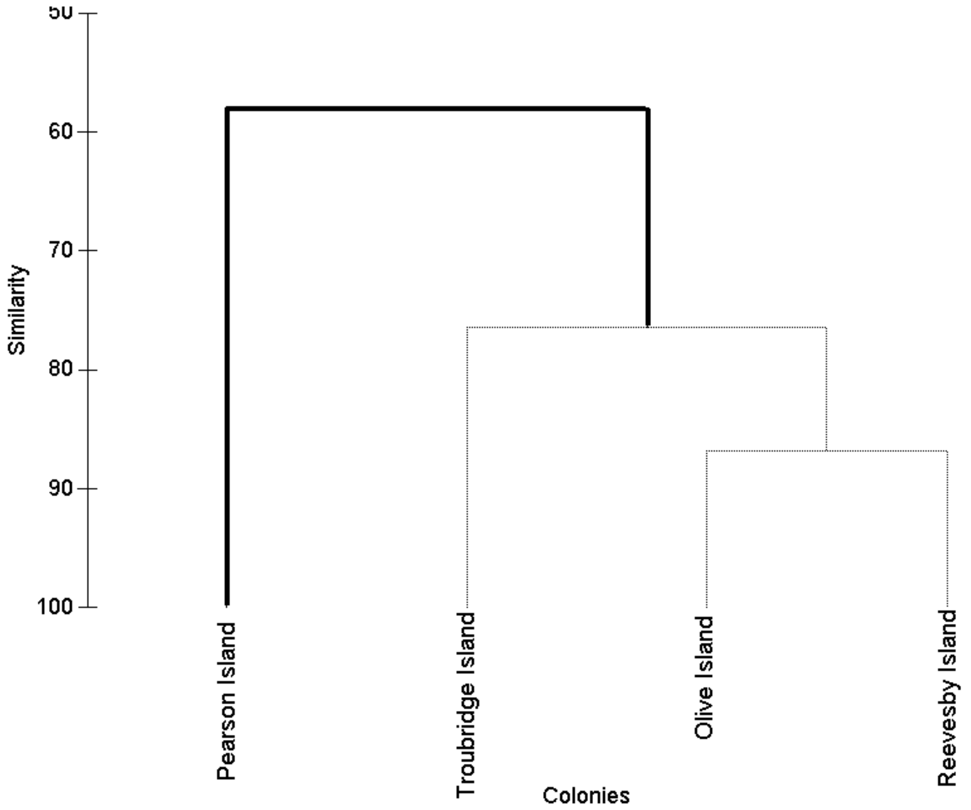

Figure 6. ANOSIM cluster dendrogram of colonies based on similarities in mean foraging parameters from each colony. Thick line separates groups that are significantly dissimilar ($P < 0.05$) and fine line signifies groups that are similar ($P > 0.05$).

Little penguins from Pearson Island were consistently further from their colony at each sequential time period of the foraging trip than little penguins from any other colony (Fig. 7). The penguins from Pearson Island reached 14.7 ± 13.9 km from the colony in the first 10 % of the foraging trip period and travelled 17.5 ± 18.5 km in the final 10 % of the foraging trip period compared with those from other colonies (2.7 - 5.7 km and 3.9 – 7.2 km respectively) ($F > 9.7$, *post hoc* LSD test, $P < 0.029$ in all cases). Penguins from all colonies made the smallest changes in distance from the colony in the middle of each foraging trip period when distances from the colony were greatest (Fig. 7). The sinuosity indices were low at all colonies (2.7 - 3.9; Table 2), where 2 is the value for a straight path out and back without deviation.

The niche overlap indices (the relative overlap in both area and time spent foraging in the area) indicated that the use (in space and time) of foraging areas by penguins at Troubridge Island was 55 % similar between 2004 and 2006, 68 % similar between 2004 and 2006, and 75% similar between 2005 and 2006. At Pearson Island, foraging was 56 % similar between 2004 and 2005.

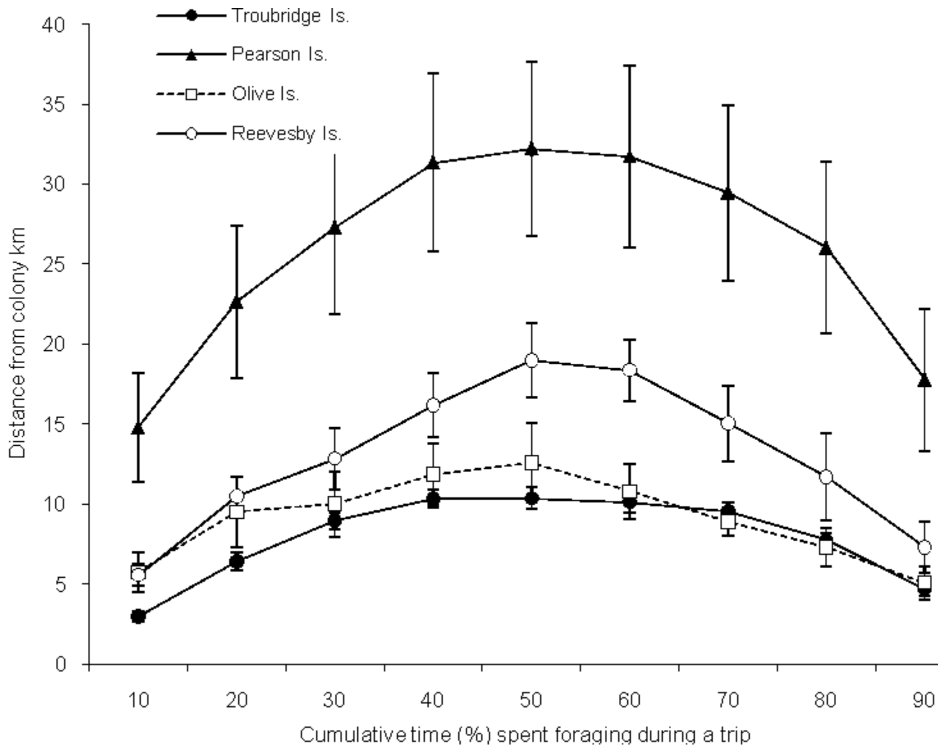

Figure 7. The mean (± S.E.) distance (km) from the colony at which penguins foraged during sequential time periods (%) of their foraging trips.

Colony foraging and body size correlations

Penguins from larger colonies travelled further (maximum and total distance) and for longer durations to forage for food (*n* = 7, r^2 = 0.9, 0.7 and 0.8 P < 0.015 in all cases, Table 3). Penguins from larger colonies also had smaller body masses and bill depths (*n* = 6 and 7, *r* r^2 = 0.7 and 0.5, P < 0.05). At colonies where penguins travelled further from the colony or for longer durations, penguins had smaller masses (*n* = 6 and 7, r^2 = 0.8 and -0.938 P < 0.015). However, none of these relationships remained significant if Pearson Island was removed from the analysis. Pair-wise comparisons indicated that Pearson Island birds had significantly longer foraging trips, travelled further (maximum and total distance), were of smaller body size (adult mass and bill depth) and fledged chicks at lower masses compared to other colonies. Breeding success (chicks that fledged per pair of penguins that laid eggs) was not significantly correlated with population size or foraging behaviour.

Table 3. Mean foraging parameters (± SD); body mass, bill size, fledging mass and breeding success (chicks that fledged per pair of penguins that laid eggs) at seven little penguin colonies. [1] denotes data from Bool *et al.* (2007), [2] denotes data from Overeem *et al.* (2006), [3] denotes data from Wiebkin (2010) and [4] denotes data from C. Gibbons (2008) unpublished data. Population estimates are the number of breeding adults.

Colony	Population	Mean max. distance from colony km (*n*)	Mean total distance km (*n*)	Mean trip duration h (*n*)	Mean bill depth mm (*n*)	Mean adult mass g (*n*)	Mean fledgling mass g (*n*)	Breeding success (*n* = years)
Pearson Is.	12000	39.2 ± 27.3 (16)	170.7 ± 180.3 (16)	64.4 ± 84.9 (15)	13.0 ± 1.2 (226)	1066.4 ± 137.8 (516)	872 ± 210.6 (212)	0.59± 0.04 (2)
Troubridge Is.	3010	13.0 ± 4.5 (24)	49.4 ± 17.2 (24)	15.9 ± 7.4 (43)	14.2 ± 1.3 (114)	1411.9 ± 246.7 (601)	1212.4 ± 206.8 (174)	0.86± 0.4 (4)
Reevesby Is.	1857	21.3 ± 5.2 (5)	64 ± 15.6 (5)	13.1 ± 1.3 (5)	13.3 ± 1.2 (126)	1367.4 ± 177.8 (130)	1135.6 ± 128.2 (9)	
Olive Is.	2290	16.8 ± 13.0 (12)	102.3 ± 191 (12)	16.0 ± 9.3 (12)	13.7 ± 1.05 (18)	1304.8 ± 196.7 (24)	1112 ± 67.5 (14)	
Granite Is.[1]	350	18.8 ± 12.9 (8)	40.9 ± 3.9 (10	23.3 ± 1.2 (10)	13.9 ± 1.3 (42)	1260 ± 157.7(42)	807 ± 208.2 (11)	0.6± 0.2 (9)
West Is. [1]	240	10.0 ± 3.4 (10)	76.3 ± 28.1(8)	13.0 ± 28.8 (8)	14.1 ± 0.9 (8)	1380 ± 84.4 (8)	1005 ± 196.1 (12)	0.8± 0.2 (5)
Penneshaw[2,3,4]	216	13.0 ± 2 (2)	66.5 ± 8.9 (2)	18.0 ± 2.3 (2)	14.0			

Environmental influences

The ranges of environmental variables in the areas where penguins foraged are presented in Table 5. SST varied by less than 1.3 °C at any colony in any year (Table 4). Chl-*a* concentration varied by 2.8 mg.m^{-3} at Troubridge Island and less than 0.7 mg.m^{-3} at the other colonies. Ranges of depth and slope were greatest at Pearson Island (91 m and 6.1 m.km^{-1}).

Table 4. The ranges of environmental variables in the cells that penguins visited around each of the four study colonies.

Environmental variables	Troubridge Island	Pearson Island	Olive Island	Reevesby Island
SST range (°C)	12.7 - 13.6 (2004) 13.3 - 14.0 (2005) 13.9 - 14.4 (2006)	15.3 - 16.6 (2004) 15.0 - 16.1 (2005)	14.3 - 15.6	12.8 - 13.6
Chl-a range (mg.m^{-3})	0.8 - 2.5 (2004) 0.5 - 2.5 (2005) 0.3 - 3.1 (2006)	0.5 - 1 (2004) 0.5 - 1 (2005)	0.8 - 1.5	0.3 - 0.5
Depth range (m)	0 - 25 (2004) 0 - 38 (2005) 0 - 33 (2006)	10 - 91 (2004) 15 - 87 (2005)	0 - 62	0 - 33
Slope range (m.km^{-1})	0.1 - 1.1 (2004) 0.1 - 0.6 (2005) 0.1 - 0.3 (2006)	0.1 - 6.2 (2004) 0.1 - 4.6 (2005)	0.1 - 2.9	0.1 - 1.1

The best GLMMs indicated that the proportional time spent in each grid area (TIA) was weakly influenced by different variables at each population (Table 5). At Troubridge Island, the top five models included interactions between chl-*a* and year, the best of which excluded all other variables. However, the best model explained only 1.6 % of the deviance from the null (intercept only) model. The best model indicated that penguins spent more time foraging in areas of lower chl-*a* (particularly in 2005). At Pearson Island, the best model indicated that penguins spent more time nearer the colony and where chl-*a* was higher. This model explained 4.0 % of the deviance from the null model. At Olive Island the top performing models included SST. The best of these explained 6.3 % of the deviance from the null model, and indicated that the interaction between cooler SST and proximity to the colony were favourable for penguin foraging behaviour. At Reevesby Island, only one model performed better than the null model, which was the interaction between SST and chl-*a*, which explained 2.7 % deviance of the null model.

Table 5. Results of the best five generalised linear mixed effects models (GLMM) with the effects of chlorophyll a (chl-a), sea surface temperature (SST), slope, distance from colony (dist), water depth (depth) and year (for Troubridge and Pearson Islands) on proportional time spent in area (TIA) by individual penguins. 'Individual' was included in all models as a random effect, environmental and physical variables were fixed effects and year was a categorical fixed effect. Notation: k = number of parameters; LL = log-likelihood; AIC = Akaike's information criterion; ΔAIC = change in AIC between the best and candidate model. The full (all factors included) and null (intercept only) models are also listed.

Model	**Colony**	**k**	**Deviance**	**LL**	**AIC**	**ΔAIC**
TIA~chl-a*year	Troubridge Is.	5	2381.29	-1201.29	2418.58	0
TIA~chl-a*year+sst*year	Troubridge Is.	8	2370.19	-1198.5	2418.99	0.41
TIA~chl-a*year+slope	Troubridge Is.	6	2378.61	-1200.85	2419.70	1.12
TIA~chl-a*year+sst	Troubridge Is.	6	2380.57	-1202.63	2423.26	4.68
TIA~chl-a*year+sst+slope	Troubridge Is.	7	2377.85	-1202.22	2424.44	5.86
TIA~year+chl-a+dist+sst+depth+slope (full)	Troubridge Is.	10	3299.88	-1219.45	2464.89	46.31
TIA~1 (null)	Troubridge Is.	1	2420.80	-1213.16	2432.33	13.75
TIA~dist+chl-a	Pearson Is.	4	3166.32	-1591.74	3193.48	0
TIA~dist+chl-a+year	Pearson Is.	6	3166.39	-1592.14	3196.28	2.80
TIA~dist+chl-a*year	Pearson Is.	5	3166.44	-1591.69	3197.38	3.90
TIA~dist	Pearson Is.	3	3174.71	-1595.14	3198.27	4.80
TIA~dist+slope	Pearson Is.	4	3171.83	-1596.88	3203.75	10.27
TIA~year+chl-a+dist+sst+depth+slope (full)	Pearson Is.	9	3163.31	-1601.76	3221.52	28.04
TIA~1 (null)	Pearson Is.	1	3298.42	-1650.51	3307.02	113.54
TIA~sst*dist	Olive Is.	3	1468.77	-746.20	1504.40	0
TIA~sst	Olive Is.	3	1521.90	-763.64	1535.28	30.88
TIA~sst+dist	Olive Is.	4	1512.79	-764.39	1538.79	34.39
TIA~sst+dist+chl-a	Olive Is.	5	1512.79	-765.72	1543.43	39.03
TIA~depth	Olive Is.	3	1532.89	-773.74	1555.49	51.08
TIA~chl-a+dist+sst+depth+slope (full)	Olive Is.	7	1505.07	-769.97	1555.94	51.54
TIA~1 (null)	Olive Is.	1	1567.81	-785.09	1576.18	71.78
TIA~sst*chl-a	Reevesby Is.	3	401.07	-201.616	415.23	0
TIA~chl-a+dist+sst+depth+slope (full)	Reevesby Is.	8	406.42	-215.387	446.77	31.54
TIA~1 (null)	Reevesby Is.	1	412.26	-207.62	421.24	6.01

Discussion

Large colonies of some central-place foraging seabirds have been shown to deplete food resources in waters near their colonies, resulting in parents having to travel further and for longer periods to provision their young (Orians and Pearson 1979, Chiaradia and Nisbet 2006). This process, known as Ashmole's halo (Ashmole 1963), can result in reductions in local prey availability, and reduced growth and survival rates of dependent young (Cooch *et al.* 1991, Croll *et al.* 2006). Distant foraging could also be a strategy to avoid intra-specific competition (Kato et al. 2008), which would be more evident in larger colonies (Dann and Norman 2006). Alternatively, the foraging behaviour of individuals and of colonies of seabirds may have more to do with local environmental and oceanographic variability, than it does with density dependent factors that underpin Ashmole's halo. My results showed a weak relationship between the distribution of foraging effort and environmental and oceanographic variables that were measured among all the colonies studied (explaining only 1.6 – 6.3 % of the variation). It is also possible that the prey around Pearson Island may be distributed further from the island as a result of factors not related to predation pressure by many penguins (e.g. predation by other predators, environmental or bottom-up trophic factors). However, for the large population of penguins at Pearson Island, the longer and more distant foraging trips in conjunction with slower chick growth rates (Chapter 3) and reduced adult body size compared with the other smaller colonies, is consistent with the expectation of localised depletion or dispersion of prey resources predicted by Ashmole's halo hypothesis. This is consistent with other studies of seabirds that have shown that the size of colonies is positively related to indices of foraging effort such as distance and duration, or negatively related to body size (Gaston *et al.* 1983, Birt *et al.* 1987, Lewis *et al.* 2001, Dann *et al.* 2006).

In this study, the use of particular areas for foraging during the breeding season remained similar over consecutive years (55 % to 75 % similar) at Pearson Island and Troubridge Island colonies. Fidelity for feeding areas has been documented in seabirds (Irons 1998, Mehlum *et al.* 2001, Kato *et al.* 2000) and more specifically in penguins (Wienecke *et al.* 2000, Ropert-Coudert *et al.* 2003, Watanuki *et al.* 2004), particularly when prey availability is stable (Barlow and Croxall 2002). Adaptable foraging strategies allow seabirds to search for and target patchy and migratory prey in changing environmental conditions, such as king penguins foraging at Heard Island (Moore *et al.* 1999). Conversely, expertise gained from fishing a specific feeding area can prove equally successful for seabirds that feed in flocks (Irons 1998) as well as individual little penguins in Western Australia (Ropert-Coudert 2003). The penguins in this study demonstrated fidelity to broad foraging areas (i.e. east of Pearson Island and generally north of Troubridge Island), either because these areas are consistently attractive for anchovy (i.e. anchovy distribution is not very patchy in penguin foraging ranges), or because previous knowledge of the areas helps little penguins forage there more successfully. These areas are probably too broad to be impacted by the predation from a large colony to cause an off-shore halo but foraging data from more years may confirm this.

Little penguins employ 'commuting behaviour', as indicated by their rapid travel before and after the diving period (active fishing) at two colonies. This behaviour is typical of most colonial animals that breed on the land and feed in the sea, such as seabirds. For example, crested terns *Thalasseus bergii* (McLeay *et al.* 2010) and cape gannets *Sula capensis* (Gremillet *et al.* 2004) commute to and from specific foraging areas where they spend most of their time. Like gannets, little penguins have adaptations that allow them to minimise the time or energy they must spend on commuting, while maximising the food returned to the breeding colony (Orians and Pearson 1979, Ydenberg 1994, Ropert-Coudert *et al.* 2004, Wilson *et al.* 2005). The greater the distance travelled from the breeding colony, the greater the food load required to balance the energy expended whilst commuting (optimal foraging theory), otherwise an individual's body condition may decline and/or dependent young may grow more slowly (Orians and Pearson 1979, Chiaradia and Nisbet 2006). Consequently, many species including penguins have evolved multiple-prey loading abilities. Alternatively because they have the prey loading capacity (e.g. a crop or large stomach), they are able to forage at greater distances (if required) than single–prey loaders such as crested terns (McLeay *et al.* 2010). By commuting to foraging areas and loading multiple prey items in their stomachs, little penguins are able to take advantage of more distant resources.

In this study, the penguins from the large Pearson Island colony (12,000 breeding penguins) exhibited maximum, mean and total distances, and trip durations that were up to 3 to 4 times greater than those of penguins from the other, smaller colonies in this study (1,800 - 3,000 penguins), as well as other colonies in previous studies including Penguin Island, Western Australia (max. range 15 - 20 km R.D. Wooller *et al.* unpublished in Ropert-Coudert *et al.* 2003), Phillip Island, Victoria (max. range 20 km, 1 - 2 days, Collins *et al.* 1999, Chiaradia and Nisbet 2006), Granite Island (max. distance 10 km, 23 h), West Island (max. distance 19 km, 16 h, Bool *et al.* 2007), and Penneshaw (max. distance 13 km, 18 h, Wiebkin 2010). The implications of parents foraging away from the colony for long periods of time are that chicks will have to fast for longer before they are provisioned. One study on Humboldt penguins *Spheniscus humboldti* found that increased energy expenditure on foraging resulted in poorer rates of offspring growth (mass and bill size), survival and reproductive success (Hennicke and Culik 2005). For any given seabird colony, there is likely to be a threshold foraging distance or duration, which determines whether parents will be able to raise chicks to fledging age or not. At Pearson Island, this threshold is much greater than previously thought for little penguins, but it is achieved by having smaller body sizes (relative to other colonies in the region), which reduces costs to furnish chicks with food.

The reason why sufficient prey densities occur at much greater distances from Pearson Island, compared to other little penguin colonies, may be because of localised prey depletion (such as Ashmole's halo). I was not able to determine the abundance of anchovy in this study, but my data suggest that penguins from Pearson Island are not able to catch sufficient anchovy near the colony to provide for their chicks. A study in the United Kingdom suggested that large populations of northern gannets can sufficiently disturb shoals of fish close to the colony, to reduce the profitability of fishing near the colony because of intraspecific competition, even without significant prey mortality (Lewis *et al.* 2001). Alternate explanations as to why localised anchovy resources near Pearson Island are not profitable for penguins may be due to local depletion by predation pressures form other marine predators. For example, Australian salmon *Arripis truttacea*, snook *Sphyraena novaehollandiae,* arrow squid *Nototodarus gouldi* and blue fin tuna *Thunnus maccoyii* (SARDI Ngerin fish sampling unpublished data, Caines 2005) may affect the abundance of anchovy around the steep bathymetric drop-offs adjacent to Pearson Island. Another possibility is that the habitat around Pearson Island is not suitable for anchovy. However, if little penguins were generalist predators as many studies have reported (Gales and Pemberton 1990, Cullen *et al.* 1992, Collins *et al.* 1999, Chiaradia *et al.* 2003), we would expect them to target a more common prey species (i.e. sardine) near the colony. If, as this thesis suggests, little penguins from Pearson Island are more specialist anchovy predators (Chapter 4), then it is surprising that the penguin population originally established on an island if low densities of anchovy surrounded it at that time.

This study indicates that even within a species, the body size of little penguins may be influenced by foraging effort, food availability and/or colony size (Chapter 3). In some albatrosses (Shaffer *et al.* 2001, Phillips *et al.* 2004), northern gannets *Morus bassanus* (Lewis *et al.* 2001) and brown boobies *Sula leucogaster* (Lewis *et al.* 2005), smaller bodied individuals appear to be better adapted to commuting large distances to foraging areas because they have lower flight costs compared with the larger birds. If this were the case for little penguins, the smaller penguins that travel further away would need to return with bigger loads to compensate for the time they spent away from their chicks. However, the little penguins at Pearson Island did not return with more food (Chapter 3), which is reflected in the small size of chicks at fledging and also lower breeding success compared with other colonies. Further, adults from Pearson Island that foraged further or for longer, or in a more sinuous (less direct) route, put on less weight and returned with less food in their stomachs. These results are consistent with the lower prey densities around Pearson Island, but are at odds with the large size of the population of little penguins at Pearson Island.

Little penguins typically forage in shallow habitats (Ropert-Coudert *et al.* 2003, Chiaradia *et al.* 2007) (e.g. penguins from Olive, Reevesby and Troubridge Islands), but some benefit (in mass gain) from foraging in deeper water (e.g. those from Reevesby Island). Because the penguins from Pearson Island rarely used water less than 50 m in depth, it is clear that the availability of shallow feeding grounds does not underpin the distribution of little penguin colonies. Given the size of the little penguin population at Pearson Island, the waters around the island clearly provide suitable little penguin foraging habitat. Similarly, Lescroel and Bost (2005) reported that breeding gentoo penguins at Kerguelen Archipelago travelled much further and for longer into deeper water at open sea sites to find suitable prey compared with those at a near-shore site that foraged near the colony. In the eastern GAB, the depth of the foraging range does not appear to affect the type of prey (anchovies) targeted by the little penguins (Chapter 5).

At Pearson Island, the fledgling size was smaller and breeding success was lower than at other colonies. Similarly, Dann *et al.* (2006) found that larger colonies produced smaller fledglings amongst eastern Australian colonies. It is worth speculating why these indices of foraging conditions and population health are negatively related to the sizes of these populations in South Australia. The foraging behaviour of little penguins from Pearson Island appears to be adapted to exploiting prey that are relatively distant and patchily distributed, compared with the prey distribution adjacent to other little penguins colonies. It may also be that the foraging behaviour of little penguins at Pearson Island is more variable in other years, outside of the two years in which I tracked penguins at this colony, and that penguins forage nearer to the island in years when prey is more abundant. However if penguins foraged nearer shore in other years, the chicks from these years should be larger, and this is not evident given the small size of adults from a range of age cohorts. Also, because there are two breeding seasons each year at this colony (and others in the region), sufficient numbers of young are produced to keep the population large, even though they fledge at smaller sizes. This is the case for large populations of thick-billed murres *Uria Lomvia* in Hudson Strait, which have similar fledging rates to smaller colonies, but the chicks fledge at lower weights (Gaston *et al.* 1983).

The influence of environmental variables on the foraging behaviour of little penguins was also significant (although not strongly), suggesting that anchovy distribution is at least partially influenced by oceanographic gradients, and that foraging behaviour by penguins is not random. Different oceanic conditions have been shown to affect foraging behaviour of seabirds in various ways. For example, different oceanographic processes of heating open water areas (wind-driven heat vs upwelling of warmer water) influenced the foraging behaviour of thick-billed murres in different sectors of the North Water Polynya (Falk *et al.* 2002). One study showed that little penguins benefit from foraging in waters with strong thermal stratification (Ropert-Coudert *et al.* 2009) where prey aggregate, and another study found they chose to forage in water with slightly warmer SST than average for the area (Hoskins *et al.* 2008). In contrast, at Olive Island, little penguins spent more time foraging in areas of cooler SST. At Troubridge and Pearson Island, little penguins concentrated their foraging in areas of slightly higher primary productivity (chl-*a*), which was also the case for crested terns (that also prey extensively on anchovy) at the same site during summer (McLeay *et al.* 2010). The abundance and distribution of clupeoids such as European anchovy *Engraulis encrasicolus* have been correlated with cooler SST and higher chl-*a* (Paloma *et al.* 2008). Because penguins commute to foraging areas by exploratory diving, they may be able to follow oceanographic gradients that help them locate prey resources. It is also likely that other factors such as benthic habitat type or prey availability (which I did not investigate), or fidelity to foraging areas influence the foraging behaviour of little penguins.

Dann *et al.* (2006) reported that little penguins on small islands have relatively high reproductive output, but because small islands have limited nesting habitat, penguins from such sites may migrate to other colonies. In the eastern GAB, the availability of nesting habitat does not appear to limit population growth. Most islands that are colonised by penguins have sparsely scattered nests, ample low shrubs and long coastlines that appear to be suitable for penguin nesting. In the eastern GAB, large populations of little penguins may be limited by food and so it is worth speculating about why, unlike gannets (Nelson 1978), individuals from these populations do not move to other, smaller colonies. Because little penguins are loyal to their feeding grounds and they generally breed at their natal colony (Stahel and Gales 1987, Marchant and Higgins 1990, Dann 1992, Priddel *et al.* 2008), the level of migration is thought to be minimal. The penguins at Pearson Island are also relatively isolated from other penguin colonies (> 80 km), making emigration by juveniles less likely. It is possible that fidelity to a large natal colony by little penguins is strengthened by strong social mechanisms that develop in large populations. These may include synchronised group associations (in good years at Phillip Island) (Daniel *et al.* 2007), individual recognition through complex vocal communication (Waas 1988, 1991), rafting at sea, and for other penguin species, synchronised fishing (Wilson *et al.* 1986, Tremblay and Cherel 1999, Takahashi *et al.* 2004).

In conclusion, this study provides evidence that penguins do not forage randomly within a given radius around their colonies, and that they forage where food is most abundant or profitable. Additionally foraging behaviour does also relate, in part, to localised environmental and oceanographic factors. Density-dependent factors such as Ashmole's halo may contribute to the regulation of large colonies by forcing parents to forage near or at their threshold foraging distance or duration, but further investigations into relative prey abundance at increasing distances from penguin colonies are needed to confirm this. A halo of depleted or unprofitable prey around at large colonies, together with the effort required by parents to forage further, may affect the amount of food returned to the chicks. The consequence of this process may be to effectively keep little penguins little at such sites.

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Chapter 7: General Discussion

This study investigated the relationships between food availability and sexual size dimorphism (SSD), chick growth strategies, diet and foraging of a permanent central-place forager, the little penguin. The foraging ecology of seabirds is constrained by the energetic requirements of the parent and dependent young, and it is also dependent on the diving, travelling, searching and prey-loading capabilities of the parents. The energy acquired by parents when provisioning chicks, particularly when chicks are older, depends on the availability of preferred prey within distances and travel times that do not exceed the fasting ability of the chicks. The choices that parents make to optimise foraging behaviour are key factors that determine their diet, energy intake and delivery to young. These ultimately determine their breeding success and fitness.

Several ecological and physiological theories provide a framework in which to discuss the key findings of this thesis. The key theories that were addressed in my thesis were that 1) a predator will adopt either a generalist or specialist feeding strategy depending on the availability of preferred prey species; 2) the growth rates of a predator will reflect the availability of food during the growth phase of development; 3) sexual size dimorphism will develop earlier if food is plentiful; 4) food availability and prey behaviour will determine foraging behaviour of a predator, and 5) a large population may deplete food around the breeding place, forcing parents to forage further from the colony, and reducing the provisioning rates to their young.

Knowledge of the variation in little penguin diet provides an understanding of their adaptability or sensitivity to changes in prey availability, the role of environmental and biological factors in shaping regional differences in diet and how variation in prey availability affects breeding success as well as growth. This thesis also discusses how bill morphology represents inter-sexual and inter-colony differences in the growth patterns of little penguin chicks and expression of SSD as a function of diet and prey delivered by parents. To determine the extent to which food availability determines the foraging strategies and energy expenditure of parents, I investigated whether other factors such as bathymetry, population size, and oceanographic conditions influenced these strategies. The dive behaviour of little penguins at sites characterised by shallow and deep water habitats provided the opportunity to investigate whether foraging strategies were driven by prey behaviour or geomorphic habitat features such as bathymetry. Finally, I addressed the relationships between foraging behaviour, colony population size and penguin body size (using bill size as a proxy) with respect to the local availability of prey.

Seabirds have adaptive feeding strategies that efficiently harvest energy within their foraging ranges and these strategies vary from specialist to generalist strategies. Generalist predators are able to switch or mix prey depending on which prey are most available. These predators are also usually less sensitive to prey fluctuations than the specialists that rely on one prey type. Specialists have well-practised strategies for finding and targeting prey but they have difficulty adapting to declines in availability of single prey types (Blake 1984). The generalist predation hypothesis predicts that the functional responses (i.e. diet switching) of generalist predators should be faster than those of specialist predators and consequently generalists have a regulating effect on prey communities (Erlinge *et al.* 1984, Klemola *et al.* 2002). Generalists have fairly stable populations, reproductive outputs and demographic structure because they switch prey when a dominant species declines in abundance (Dupuy *et al.* 2009). This compares with the reproductive output and population size of a specialist, which fluctuates in response to the increases and decreases in prey abundance (Dupuy *et al.* 2009). I found that little penguins in South Australia primarily ate anchovy with little spatial and temporal variation in diet. In South Australia, anchovy are abundant and broadly distributed over a range of shelf and gulf habitats (Dimmlich *et al.* 2009) so that little penguins can function more as anchovy specialists. As such, penguin breeding success and population demography are likely to reflect variation in anchovy availability in South Australia. In other regions, the diets of little penguins are more diverse temporally, and are dominated by different prey species, such as sardine, garfish, barracouta, blue grenadier, sandy sprat and squid, as well as anchovy (Klomp and Wooller 1988, Montague and Cullen 1988, Gales and Pemberton 1990, Cullen *et al.*1992, Chiaradia *et al.* 2003, Chiaradia *et al.* 2010).

The selective preference for anchovy by little penguins in this study is surprising because sardines are known to be equally, if not more, abundant in the eastern Great Australian Bight (Ward *et al.* 2001, Dimmlich *et al.* 2009). In this region, crested terns consume similar amounts of sardine and anchovy (McLeay *et al.* 2009). Just 800 km to the east, at colonies in Victoria, sardine were once a major prey species of little penguins and Australasian gannets *Morrus serrator* during summer breeding seasons (Bunce and Norman, 2000, Cullen *et al.* 1992, Chiaradia *et al.* 2010). Perhaps, for little penguins in the eastern GAB, the high-energy value of juvenile anchovy (Chapter 4) may influence their choice. Furthermore, differences in catchability or availability may also exist in the top 13 m of the water column (within which penguins dive) particularly during winter months when sardines are known to migrate lower in the water column (Gomon *et al.* 2008). Because little penguins elsewhere are considered more generalist predators, the species evidently does have capabilities to adapt to changes in prey species availability. It is unclear how adaptable little penguins in South Australia would be to marked fluctuations in anchovy availability (Crawford and Shelton 1978, Tasker *et al.* 2000).

In South Australia, anchovy are known to be widely distributed across the eastern GAB and to spawn in both shelf and gulf waters all year-round with peak spawning in the summer months (Ward *et al.* 2001, Dimmlich *et al.* 2004). Surveys indicate that juveniles migrate from nursery areas at the top of the gulfs out to the shelf waters, as they grow older and larger (Dimmlich *et al.* 2006). The diet of little penguins in the region reflects the wide availability of juvenile anchovy year-round and therefore widespread fish spawning. The consistency in anchovy size consumed by penguins within any time period, and within a colony also points to the consistent availability of specific sizes and ages-classes of fish. Furthermore, the greatest consumption of juvenile anchovy by little penguins, occurred during the winter breeding season, when the fish were of an age or size indicative of being spawned during the previous summer (calculated from Dimmlich and Ward 2006, Cullen *et al.* 1992). Penguin diets at Troubridge Island also reflect migratory movement of juvenile anchovy cohorts through lower Gulf St Vincent (Dimmlich and Ward 2006). We may speculate that penguins living in Spencer Gulf (e.g. at

Wardang Island and Sir Joseph Banks Islands) have similar diets and breeding success, to those penguins at Troubridge Island because anchovy migration may be similar in both gulfs. The movements of juvenile anchovy spawned on the shelf remain a mystery and more research into anchovy is needed to understand penguin-prey interactions.

The diets of other bird species, including elegant terns *Sterna elegans*, Cape gannets *Sula capensis* and brown pelicans *Pelecanus occidentalis californicus* have been used as indicators of spatial and temporal changes in the abundance of commercially exploited and ecologically important prey species (Anderson and Gress 1982, Berruti and Colclough 1987, Montevecchi and Myers 1995, Verlade *et al.* 2004). Continued monitoring of the variability in penguin diet may provide further insights into changes in the distribution, movement, abundance and spawning chronology of the anchovy across the region, especially when the patchy distribution of fish schools makes them difficult to monitor directly. Further monitoring of penguin diet will also determine whether changes in diet or delivery of food as a consequence of shifts in food availability will lead to penguins gradually becoming smaller.

Two of the most ecologically important fish species in temperate pelagic ecosystems are anchovy and sardine because they are consumed in large biomasses by marine predators (Crawford and Shelton 1978, Parrish *et al.* 1999, Schwartzlose *et al.* 1999, Furness 2003, Ward *et al.* 2001, Ward *et al.* 2006, Dimmlich *et al.* 2004, Dimmlich *et al.* 2009). In South Australia, competition between these two fish species is thought to lead to spatial separation where sardines force anchovies into inshore waters of higher salinities and temperatures (Ward *et al.* 2001, Barange *et al.* 2009). Compared with the changeable environmental conditions of offshore waters, the inshore gulf environments in South Australia are relatively stable. It is the gulf environments that support a large reserve of young anchovies (Dimmlich et al 2009). Because the majority of penguin colonies in South Australia are located on islands in these inshore areas, anchovy distribution and abundance may have influenced the persistence and growth of these colonies.

However, the region's largest penguin colony (Pearson Island) is located in off-shore shelf waters where sardines are thought to predominate (Ward *et al.* 2001). In these off-shore shelf waters, penguins appear to still be able to selectively target sufficient anchovy (Chapter 4 and 5). Similarly, other species such as Guanay cormorants relied on anchovies off western South America in the 1970s, even when sardines were available (Furness and Monaghan 1987). Furness and Monaghan (1987) indicated that sardine stocks were insufficient to prevent the decline of cormorant populations following a local crash in the anchovy stock. Throughout my study in South Australia and since the mass mortality of sardines in 1998, the abundance of sardines has increased (Ward *et al.* 2008). It would be interesting to determine whether a continued increase in sardine stocks will affect the abundance and or distribution of anchovy and, in turn, the health and status of little penguin populations or a change in penguin sizes.

The availability of food appears to influence the provisioning strategies of parents and therefore the growth of dependent young (Badyyaev 2002). Increased prey availability is responsible for the enhanced growth in blackbird chicks that were experimentally swapped from nests in areas with reduced food (James 1983). Similarly, decreased prey resources (resulting from disease-related mass mortality of sardine stocks) resulted in small bills of crested terns *Thalasseus bergii* chicks which persisted throughout adulthood (McLeay et al. 2009). I found that the growth of little penguin bills was greatest in colonies where local prey availability was higher, and this accelerated growth was also reflected in the size of adult bills. This could be tested with a chick-translocation experiment in a large colony where populations are not declining and where any risk of translocation failure would not affect population stability. Other studies support this relationship where reductions in food availability affect the growth rates of little penguin chicks (Wienecke *et al.* 2000, Chiaradia and Nisbet 2006) although the final size of these chicks, as adults, was not reported. Reduced food availability over thousands of years may have been a factor that has selected for small size in many animals (Watt 2010 and references within), including modern penguins (Williams 1995, Baker 2006).

Parents may also vary or regulate provisioning rates depending on the sex of the young as well as on the availability of food. Parents have been shown to preferentially provision one sex over another in some bird species, including brown songlarks *Cinclorhamphus cruralis* (Magrath *et al.* 2007) and marsh harriers *Circus aeruginosus* (Krijgsveld *et al.* 1998). In some cases for seabirds, when male young are provisioned more, they grow larger than their sisters while they are dependent (Scolaro 1987, Bretagnolle and Thibault, 1995). Preferential provisioning to one sex may only occur when food availability is high, (Schauroth and Becker, 2008), and may also result in more pronounced SSD of young (Badyyaev 2002). My data suggest that SSD was only expressed in the bills of fledglings under favourable nutritional conditions. The provisioning strategies that result in early development of SSD in little penguins are not understood, but they could be tested using controlled feeding trails. The benefits (if any) of early development of SSD on fitness, including foraging success, age at first breeding and breeding success is unclear, but provides fertile ground for future research.

To my knowledge, sexual size dimorphism has not been reported elsewhere for little penguins before fledging age (Renner and Davis 1999), but SSD has been reported in the chicks of many other seabirds, such as Magellanic penguins *Spheniscus magellanicus* (Scolaro 1987) and Cory's shearwaters *Calonectris diomedea* (Bretagnolle and Thibault, 1995). In other seabirds such as common terns *Sterna hirundo*, differential growth rates occur between male and female young only in years when prey availability is optimal (Becker and Wink, 2003, Schauroth and Becker, 2008). Rapid growth rates of chicks may improve survival (Ludwigs and Becker 2006), by allowing them to fledge earlier or in better condition, or to provide them with energy stores while they learn to provide for themselves (Starck and Ricklefs 1998). Rapid growth rates of chicks may also lower the age at reproductive maturity and ultimately increase the reproductive fitness of these individuals (Becker *et al.* 2001).

The fasting ability of young is an important factor that limits the foraging range of adult seabirds during the provisioning period. Central-place foragers forage near the colony during the period that they are provisioning their young. During this time, provisioning adults might compete with other adults for prey, as is the case for gentoo penguins (Wilson *et al.* 1998). Species that forage far from the colony such as short-tailed shearwaters *Puffinus tenuirostris* provision their chicks infrequently but their chicks are adapted to both receiving large meals and also to fasting for long periods (Weimerskirch and Cherel 1998, Weimerskirch 1998). Seabirds such as penguins forage nearer their colony because their young require food regularly to maintain a relatively fast and steady growth rate (Collins *et al.* 1999, Wienecke *et al.* 2000). Feeding locally has implications for penguins if the food availability becomes unreliable or decreases. These are common consequences of commercial and recreational fishing, as well as climate change. Little penguins can evidently adapt to expand their foraging range further than previously thought (i.e. at Pearson Island) but the growth of their chicks is disadvantaged as a result of the less frequent meals. However, at Pearson Island it is clear that some chicks survive to reproduce successfully, so travelling further is still a viable option for parents.

Large colonies of seabird species can deplete food stocks close to the colony (Birt *et al.* 1987), a phenomenon known as Ashmole's halo (Ashmole 1963). A halo of depleted food often forces breeding birds to forage further away and for longer (Birt *et al.* 1987, Lewis *et al.* 2001). This may have occurred at the largest colony of penguins in South Australia where penguins forage three times further away from their colony and for three times the duration than those at colonies with smaller populations. In other seabird species, greater foraging distances and durations can reduce chick growth rates (Waugh *et al.* 2000, Waugh *et al.* 2003, Watanuki *et al.* 2004, Hennicke and Culik 2005). Colonial breeding is thought to convey social and protective benefits to seabirds, but if populations expand and deplete the availability of prey near their colony, intra-specific competition may then regulate the population size (Birt *et al.* 1987). Because there appears to be limited resources surrounding Pearson Island, the repercussions of travelling further and for longer appear to be poorer chick growth (relative to other colonies in the region), and reduced adult size.

One of the most unusual aspects of the ecology of little penguins in the western part of their range is that they breed throughout winter (Klomp et al 1991, Johnson and Wiebkin 2008). Penguins in Tasmania, Victoria and New Zealand, breed during spring and summer (Stahel and Gales 1987, Goldsworthy *et al.* 2000, Chiaradia *et al.* 2003, Miyazaki and Waas 2003, Weerheim *et al.* 2003, Robinson *et al.* 2005). Breeding in winter for little penguins brings challenges such as reduced daylight for diving (Chapter 5) and rougher oceanic weather in which to forage. Anchovy availability in winter must outweigh these challenges. A possible benefit of breeding in winter is that it reduces the impact of hot temperatures on surface-nesting penguins (Klomp *et al.* 1991). Available prey is probably the main factor for the onset of breeding, which appears to differ between regions (east and west of the range). Further, the different breeding phenology may lead to genetic differences between regions (Overeem 2005, Overeem *et al.* 2007) or the evolution of subspecies (Roeder *et al.* 2001, Peucker *et al.* 2009). The protracted winter breeding in South Australia and Western Australia may also offer increased opportunities for breeding, such as double clutching which was found to be common at these colonies (R. Brandle, N. Gilbert, A. Wiebkin unpublished data). Favourable conditions for breeding in winter are also reflected in the higher fledging success (number of chicks fledged per egg hatched) at Troubridge and Pearson Islands (0.8 and 0.7, Chapter 6), and at Penguin Island, Western Australia (0.7) (Wienecke *et al.* 1995) compared with spring/summer breeding penguins at Phillip Island, Victoria (0.5) (Chiaradia *et al.* 2007). The resource base in South Australian waters during winter may, infact, be better for little penguins than that of waters further east.

Seabirds that eat a diversity of prey are less affected by a decrease in the abundance of any one type of prey than those that eat only one or a few prey types. Little penguins in South Australia that have a selective diet may be more vulnerable to changes in prey abundance. If anchovies became less available in the winter breeding season, then results from this thesis suggest that little penguins would target garfish (Chapter 4). The effects of this on the timing, onset and success of penguin breeding, is not known. Effects may be particularly detrimental at Pearson Island where there is very little seafloor habitat shallow enough to support extensive seagrass beds preferred by garfish (Gomon *et al.* 2008, Chapter 5). Additionally, this could result in higher intra-specific competition for a variety of prey within the relatively small seagrass habitats around island colonies (Gulf St Vincent: Tanner et. al. 2005). Even though garfish are larger and possibly easier to catch, the lower calorific value of garfish (Chapter 4) probably means that penguins would need to catch more to maintain the concomitant chick growth rates and breeding success, thereby creating further intra-specific pressures in these seagrass habitats.

Future research

This thesis provides data to enhance the management of the marine ecosystem in South Australia. Spatial models of little penguin consumption and use of habitat will be developed from these data to inform management of at-sea resources for little penguins. Further, the diets of little penguins will contribute to trophic models of the ecosystem (Goldsworthy *et al.* 2010), which can then be used to identify trophic guilds or groups containing species with similar ecosystem functions (Daly 2007). On-going management of pelagic ecosystems also relies on the ability to detect change. Long-term investigations into little penguin diets are likely to reflect changes to anchovy abundance and the clupeoid community. Similarly, growth parameters such as bill size across cohorts and foraging parameters such distance and duration will reflect long-term (over several years) and short-term (daily-weekly) food availability, respectively.

The age of a seabird can influence both its diet, as has been shown for crested terns (McLeay *et al.* 2009) and the growth of herring gulls (Coulson *et al.* 1981), however, few studies know the age of the seabirds being researched. Age-related differences in the diets of little penguins in South Australia are not known, however the predominance of anchovy in this study suggests that penguins of all ages consume similar diets across the eastern GAB. The implications on age at first breeding, breeding success and foraging success are not understood for little penguins but it is worth investigating whether early development of SSD in some penguins influences these variables. To address some of these ecological consequences, a general improved understanding of SSD and the provisioning strategies that lead to SSD in chick growth is needed.

A fine scale understanding of the habitats used by little penguins is required to better protect their critical foraging grounds. I used platform terminal transmitters (PTTs), which are accurate to between 200 m and 5 km (Chapter 6), with ~13 locations recorded per day, as well as dive loggers that do not record habitat information. Other researchers have been able to identify fine-scale habitat use of larger species such as emperor penguins equipped with combinations of PTTs and dive loggers (Rodary *et al.* 2000). Similarly, GPS trackers have been used to obtain highly accurate positions on African penguins *Spheniscus demersus* (Ryan *et al.* 2004) and crested terns (McLeay 2010). Ropert-Coudert *et al.* (2009) recently used accelerometers and dive loggers together on little penguins and found that they seek thermal stratification in the water column to target fish. Such fine-scale habitat studies will allow us to better manage and protect seabird resources with further advances and miniaturisation of tracking devices (Preston *et al.* 2010).

This thesis has highlighted the variation in foraging behaviour within and between colonies. Within colonies, breeding penguins foraged in the same broad areas each year but between colonies, the size of these areas differed significantly. Despite natural variation in prey abundance and distribution, penguins appear to rely on experience and knowledge of these particular foraging areas to catch fish. More years of tracking data, particularly in years of varying prey abundance is required to determine the ability of penguins to alter their foraging strategies in response to changes in prey availability.

The foraging behaviours of many seabirds are known to vary between breeding and non-breeding periods (Weavers 1992, Collins et al 1999), between breeding stages (Moore *et al.* 1999, Dann *et al.* 2007) and between sexes (Clarke *et al.* 1998, Kato *et al.* 1999, Lewis *et al.* 2005). During the breeding season, adult little penguins use feeding grounds that are close to their colonies (Collins *et al.* 1999, Hoskins *et al.* 2008) but adult little penguins may forage further away when not provisioning chicks (Collins *et al.* 1999). This has not yet been measured in South Australia. Juvenile penguins are infrequently observed in the colony (Dann and Cullen 1990, Wiebkin 2010) and, for juveniles, extended time at sea also provides opportunities to forage further from the colony. The foraging behaviour of juvenile little penguins remains unstudied, because the retrieval of satellite transmitters is probably much less reliable compared to breeding adults. Sex differences in foraging behaviour have been described for some cormorants (Kato *et al.* 1999, Fonteneau *et al.* 2009), albatrosses (Phillips *et al.* 2004) and penguins (Clarke *et al.* 1998), many of which are sexually size dimorphic species. The evidence for sexual segregation at-sea in little penguins is sparse (Ropert-Coudert *et al.* 2003) and this would be clarified with larger sample sizes. Differential selection of foraging areas by penguins in different breeding stages, or by penguins of different age groups and sexes, may reduce intraspecific competition in particular habitats. If this is the case, the foraging areas used by all penguins at a colony, including the non-breeding and juvenile penguins may be more expansive than this thesis suggests.

The first censuses of little penguin populations in the South Australian region were done in the 1990s (R. Brandle and N. Gilbert unpublished data). From the populations that have been monitored in recent decades, one has remained stable (Troubridge Island) (Wiebkin 2010, Kinloch *et al.* unpublished data), and four populations have decreased (Granite Island, West Island, Kingscote and Penneshaw) (N. Gilbert unpublished data, M. Kinloch *et al.* unpublished data). There has been a general decline in abundance in some areas (Encounter Bay and Kangaroo Island) and some colonies have all but gone (West Island reduced from ~4000 in 1992 to a handful in 2011), some on Kangaroo Island, and some amongst Sir Joseph Banks Islands (a few thousand 5 years ago to a handful in 2011 on Spilsby Island; W. Goedseke pers. comm.). Monitoring of little penguin colonies is warranted, even where populations are not currently declining. Censuses of regionally-representative colonies each year would be appropriate to inform management decisions for conserving little penguins in South Australia. Goldsworthy *et al.* (2007) used a distance matrix to identify regional clusters of Australian sea lions *Neophoca cinerea* to underpin survey designs and the lack of data about Australian sea lion population substructure. Because the population structure of little penguins is not well understood, a similar approach to the identification of potential subpopulations of little penguins would be useful in South Australia. Surveys should be at a time that is relative to the peak or onset of the breeding season.

While six of the populations in this study either appear stable or have insufficient data to determine population trends, two (Granite and West Islands) have declined Bool *et al.* 2007). Other colonies near urban areas are also declining including

Kingscote and Penneshaw (Kangaroo Island; KI NRM unpublished census data 2011). Recent data suggests that some fur seals near these declining colonies eat penguins (Page *et al.* 2005, Baylis *et al.* 2006, Bool *et al.* 2006). There is substantial public pressure to relocate, disturb or cull fur seals because they are perceived to be the cause of these declines. However, no studies have quantified the impact of fur seals on little penguin populations. Projects that can address these issues would include a targeted study on the number of penguins actually being consumed, through seal faeces analysis and a study modelling the at-sea overlap in habitat used by fur seals and penguins. Other investigations into rat and cat predation, human disturbance and food (anchovy) resources would also address potential causes of these declines (Klomp 1991, Bool *et al.* 2007).

My thesis identified the reliance of little penguins on Australian anchovy in the eastern Great Australian Bight, and suggests these populations would be sensitive to reductions in anchovy stocks if fisheries began targeting these fish. The study highlighted the roles of environmental, ecological and biological factors in shaping different foraging strategies within the constraints of chick provisioning, dive capabilities and daylight length. Understanding these relationships further will underpin future management of penguins in the region.

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Appendix 1. Summary of body mass, sex and foraging parameters of little penguins deployed with satellite transmitters at four colonies.

colony	year	bird #	sex	wt before g	wt after g	trip duration hrs	total distance km	max distance from colony km	mean distance from colony km ± S.D.	mean water depth m ± S.D.	mean slope of seafloor ± S.D.	mean travel speed km.h^{-1} ± S.D.	median bearing	# cells entered	# filtered track segment	sinuosity index
Troubridge Is.	2004	1	m	1410	1420	14.4	42.2	8.1	3.7 ± 1.9	6.9 ± 6	0.1 ± >0.1	2.6 ± 2	32	34	13	5.2
Troubridge Is.	2004	2	f	1280	1210	14.5	28.9	6.3	2.8 ± 1.8	7.6 ± 5.1	0.1 ± >0.1	2.1 ± 1.8	319	22	13	4.6
Troubridge Is.	2004	3	m	1230	1310	14.5	39.6	10.9	5.1 ± 1.6	3.9 ± 3.6	0.1 ± >0.1	1.1 ± 1.6	14	25	7	3.6
Troubridge Is.	2004	4	f	1550	1460	14.5	33.1	12.6	5.9 ± 4.3	6.2 ± 4	0.1 ± 0.1	2.1 ± 1.3	25	33	9	2.6
Troubridge Is.	2004	5	f	1160	1180	12.8	44.1	14	7.8 ± 4.1	1.6 ± 4.2	0.1 ± >0.1	2.7 ± 1.9	20	40	10	3.1
Troubridge Is.	2004	6	m	1440	1220	15.2	20.8	7.4	4.2 ± 2.6	5.7 ± 4.6	0.2 ± 0.1	1.1 ± 0.8	15	16	9	2.8
Troubridge Is.	2004	7	m	1190	1270	15.1	46.8	9.6	5.3 ± 2.7	12.1 ± 5.9	0.1 ± 0.1	3 ± 1.8	19	39	14	4.9
Troubridge Is.	2004	8	m	1450	1430	14.5	67.2	18.1	4.9 ± 3.8	10.7 ± 4.8	0.1 ± >0.1	3.4 ± 2.7	315	67	11	3.7
Troubridge Is.	2004	9	m	1370	1560	15.1	71.3	10	5.8 ± 2.6	6 ± 3.8	0.1 ± >0.1	5.1 ± 1.6	335	73	11	7.2
Troubridge Is.	2004	10	f	1110	1160	15.4	38.5	13.2	6.3 ± 3.6	12.9 ± 4	0.1 ± >0.1	1.8 ± 1.4	18	35	8	2.9
Troubridge Is.	2004	11	f	1050	1240	15.4	47.5	13.6	8.4 ± 4	5.4 ± 4.1	0.1 ± >0.1	3.1 ± 2.5	356	51	9	3.5
Troubridge Is.	2004	12	f	1100	1240	14.2	66.4	14.4	8 ± 2.9	18.1 ± 7.6	0.1 ± >0.1	4.4 ± 3.2	27	48	15	4.6
Troubridge Is.	2004	13	m	1480	1610	14.5	54.9	8	4 ± 2.3	1.4 ± 1.5	0.1 ± >0.1	3.7 ± 2.8	324	37	11	6.9
Troubridge Is.	2004	14	m	1280	1450	14.9	70.8	17.3	10.5 ± 4.1	1.2 ± 1.3	0.1 ± >0.1	4.2 ± 2.8	331	74	14	4.1
Troubridge Is.	2004	15	f	1030	1145	13.4	44.2	13.8	8.5 ± 4.3	4.2 ± 5.9	0.1 ± >0.1	3.5 ± 2.4	34	48	12	3.2
Troubridge Is.	2004	16	m	1310	1340	15.2	57.9	15.1	9.9 ± 5	0.8 ± 1.5	0.1 ± >0.1	3.8 ± 2.7	342	48	18	3.8
Troubridge Is.	2004	17	f	1100	1200	14.5	29.1	8.2	4.2 ± 2.5	4.4 ± 4.4	0.1 ± >0.1	1.8 ± 2.2	23	21	9	3.5
Troubridge Is.	2004	18	f	1160	1350	14.5	41.9	10.3	6.9 ± 3.2	6.6 ± 3.7	0.1 ± >0.1	2.5 ± 3.7	59	36	12	4.1
Troubridge Is.	2004	19	m	1300	1660	14.2	37.6	11.7	7 ± 4	10.8 ± 4.7	0.1 ± >0.1	2.3 ± 1.7	342	33	12	3.2
Troubridge Is.	2004	20	m	1240	1370	14.5	39.3	14.2	9.2 ± 4.5	10.6 ± 5.7	0.1 ± >0.1	3.1 ± 2.2	221	43	12	2.8
Troubridge Is.	2004	21	m	1140	1350	14.5	31.3	10.7	6.5 ± 3.6	6.4 ± 2.1	0.1 ± >0.1	1.8 ± 1.1	334	31	10	2.9
Troubridge Is.	2004	22	f	1160	1200	14.5	56.8	11.9	5.2 ± 3.2	6 ± 3.8	0.1 ± >0.1	2.9 ± 3	323	51	13	4.8
Troubridge Is.	2004	23	m	1400	1590	13.7	46.4	8.1	5.2 ± 2.1	2.3 ± 2.7	0.2 ± 0.1	3.4 ± 2.2	328	33	11	5.8

colony	year	bird #	sex	wt before g	wt after g	trip duration hrs	total distance km	max distance from colony km	mean distance from colony km ± S.D.	mean water depth m ± S.D.	mean slope of seafloor ± S.D.	mean travel speed km.h^{-1} ± S.D.	median bearing	# cells entered	# filtered track segment	sinuosity index
Troubridge Is.	2004	24	m	1310	1310	13.8	34.6	9.2	5.7 ± 2.8	1.6 ± 2.9	0.1 ± >0.1	1.9 ± 1.3	290	32	13	3.7
Troubridge Is.	2005	25	m	1230	1410	15.2	52.4	11.3	7.1 ± 3.5	7.9 ± 6.1	0.1 ± >0.1	3.4 ± 2.5	53	53	12	4.6
Troubridge Is.	2005	26	m	1280	1460	15.2	57.9	17.9	11.4 ± 5.7	18.6 ± 10	0.1 ± 0.1	3.8 ± 2	202	50	18	3.2
Troubridge Is.	2005	27	f	1360	1170	13.9	34.3	13.6	8.5 ± 3.9	11.7 ± 4.9	0.1 ± 0.1	3.1 ± 2	107	32	12	2.5
Troubridge Is.	2005	28	m	1250	1540	15.2	61.5	16.5	8.4 ± 4.2	18.3 ± 10.6	0.1 ± 0.1	3.7 ± 2.3	21	53	14	3.7
Troubridge Is.	2005	29	m	1420	1410	15.2	45.2	12.8	8.1 ± 4	3.8 ± 5.3	0.2 ± 0.1	2.8 ± 2.3	23	44	15	3.5
Troubridge Is.	2005	30	f	1320	1130	15.2	54.1	13.1	8.6 ± 3.8	17.8 ± 10.1	0.1 ± 0.1	3.4 ± 1.9	179	42	13	4.1
Troubridge Is.	2005	31	m	1230	1440	63.3	119.5	26.2	11.7 ± 6.6	9.4 ± 6.4	0.1 ± >0.1	3.2 ± 2.1	146	104	31	4.6
Troubridge Is.	2005	32	f	1270	1250	15.4	80.9	29.7	8.8 ± 7.5	22.9 ± 11.4	0.1 ± 0.1	4.3 ± 2	161	76	12	2.7
Troubridge Is.	2005	33	m	1190	1370	15.2	32.1	10.7	6.4 ± 3.6	23.6 ± 10.4	0.1 ± 0.1	1.9 ± 1	20	34	8	3
Troubridge Is.	2005	34	f	1390	1260	15.2	36.7	11.4	6.5 ± 4.3	10.6 ± 6.1	0.1 ± >0.1	2.5 ± 2.1	25	31	15	3.2
Troubridge Is.	2005	35	m	1520	1540	15.3	42.5	15.5	8.2 ± 4.6	9.4 ± 6.2	0.1 ± >0.1	2.5 ± 1.3	198	41	13	2.7
Troubridge Is.	2005	36	f	1200	1190	15.3	52.2	16.3	9 ± 5.1	19.9 ± 8.3	0.1 ± 0.1	3.8 ± 2	207	53	11	3.2
Troubridge Is.	2005	37	m	1310	1350	15.2	47.7	13.9	8 ± 4.2	24.6 ± 12.9	0.1 ± 0.1	3.3 ± 2.1	334	48	10	3.4
Troubridge Is.	2005	38	f	1350	1230	17.1	54.2	14.7	8.9 ± 4.8	18.3 ± 12.9	0.1 ± 0.1	3.3 ± 2.3	212	51	14	3.7
Troubridge Is.	2005	39	m	1420	1350	14.2	52.8	13.7	7.5 ± 4.3	4.4 ± 4.3	0.1 ± >0.1	3.7 ± 2.2	28	51	15	3.8
Troubridge Is.	2006	40	m	1320	1600	14.5	40.6	8.8	5.3 ± 2.9	8.9 ± 4.8	0.1 ± >0.1	2.4 ± 1.6	45	34	13	4.6
Troubridge Is.	2006	41	m	1290	1310	14.5	70.9	11.3	6.4 ± 3.9	8.5 ± 6.4	0.1 ± >0.1	5 ± 2.5	71	65	15	6.3
Troubridge Is.	2006	42	m		1210	14.5	45.6	10.5	6.1 ± 3	10.5 ± 5.2	0.1 ± >0.1	2.9 ± 1.9	54	36	17	4.3
Troubridge Is.	2006	43	m	1100	1100	14.5	51.1	15.4	7.1 ± 3.6	18 ± 8	0.2 ± 0.1	3.5 ± 4	105	45	15	3.3
Pearson Is.	2004	44	f	1230	1000	179.4	400.6	87.6	62.1 ± 20.6	43 ± 17.6	1.2 ± 0.5	2.2 ± 2.1	82	334	128	4.6
Pearson Is.	2004	45	f	900	1050	11.8	39.1	16.4	11.2 ± 5	65 ± 16.8	0.4 ± 0.5	3.6 ± 2.4	123	45	8	2.4
Pearson Is.	2004	46	f	1040	890	179.4	409.6	77.5	50.5 ± 18	50.5 ± 21.1	0.4 ± 0.7	2.5 ± 2	88	358	112	5.3
Pearson Is.	2004	47	m	1160		300	605.9	74.1	47.2 ± 15.4	75.6 ± 14.2	0.2 ± 0.4	2.3 ± 2.3	105	531	164	8.2
Pearson Is.	2004	48	f	1000	1030	11.8	44.1	13.6	8 ± 4.1	69.6 ± 6.7	0.1 ± 0.2	3.7 ± 1.8	123	52	10	3.2

colony	year	bird #	sex	wt before g	wt after g	trip duration hrs	total distance km	max distance from colony km	mean distance from colony km ± S.D.	mean water depth m ± S.D.	mean slope of seafloor ± S.D.	mean travel speed km.h^{-1} ± S.D.	median bearing	# cells entered	# filtered track segment	sinuosity index
Pearson Is.	2004	49	m		1120	59.8	48.3	11.8	6.7 ± 2.7	77.2 ± 4.9	0.1 ± 0.1	4.7 ± 1.7	182	59	12	4.1
Pearson Is.	2004	50	f	950	*			73.2	35 ± 19.5	70.9 ± 20.9	0.3 ± 0.6	3.3 ± 1.4	142	115	26	1.3
Pearson Is.	2004	51	m	1140	1150	11.8	110.1	14.2	8 ± 4.8	75.1 ± 16	0.5 ± 0.9	3.6 ± 1.9	94	45	7	7.8
Pearson Is.	2004	52	f	1000	1010	11.8	63.6	14.6	6.2 ± 4.7	77.9 ± 8.9	0.1 ± 0.2	6.4 ± 2.9	92	56	12	4.4
Pearson Is.	2004	53	m	1280	1250	35.9	50	16.1	2.1 ± 2.6	64.9 ± 24.1	0.4 ± 0.7	5.3 ± 7.5	130	45	11	3.1
Pearson Is.	2004	54	m	900	*				4.5 ± 1.9	54.3 ± 29.2	0.9 ± 1.4	6.9 ± 3.7	106	11	4	1.3
Pearson Is.	2005	55	m	1070	1000	12.1	59.5	21.2	12 ± 6.3	73.8 ± 14.6	0.3 ± 0.5	5.8 ± 2.2	108	67	11	2.8
Pearson Is.	2005	56	f	900	1070	36.1	136.8	52.4	34.5 ± 15.9	75.8 ± 8.2	0.2 ± 0.3	4.6 ± 2.1	105	146	27	2.6
Pearson Is.	2005	57	m	1140	1100	36.7	160	57.4	38.6 ± 15.9	66.4 ± 7.4	0.1 ± 0.2	5.3 ± 3.8	83	180	32	2.8
Pearson Is.	2005	58	f	1110	1130	12.2	85.3	26.1	13.5 ± 8.3	69.8 ± 20.3	0.5 ± 0.9	6 ± 2.1	110	100	8	3.3
Pearson Is.	2005	59	f	900	860	108.1	416.9	62.7	43.4 ± 15.1	72.4 ± 9.8	0.1 ± 0.4	4.3 ± 2.2	96	304	110	6.6
Pearson Is.	2005	60	m	940	1150	12.2	52.1	23.1	12.9 ± 7.2	73.7 ± 22.7	0.3 ± 0.5	5.2 ± 1.9	137	65	9	2.2
Pearson Is.	2005	61	m	1110	980	12	49.8	24.7	15.1 ± 7.3	74.7 ± 11.4	0.2 ± 0.3	5.8 ± 1.9	100	39	8	2
Olive Is.	2006	62	f	1030	1320	11.9	26.5	8.7	5.5 ± 1.6	50.6 ± 9.3	0.2 ± 0.3	2 ± 1.4	187	22	11	1.6
Olive Is.	2006	63	m	1090	1320	11.9	36.4	12	7.5 ± 3.6	45 ± 16	0.2 ± 0.2	3.5 ± 2	144	39	10	3.6
Olive Is.	2006	64	f	1080	1290	12	43.1	10	6.9 ± 3.1	21 ± 18.8	1.1 ± 0.9	3.6 ± 2	104	30	13	3.1
Olive Is.	2006	65	m	1120	1340	11.9	42.1	11.3	5.3 ± 3.4	41.7 ± 15.4	0.4 ± 0.4	3.7 ± 2.6	161	38	13	3.4
Olive Is.	2006	66	f	1150	1180	11.8	57.4	24.1	9.5 ± 6.8	47.8 ± 15.7	0.2 ± 0.3	4.9 ± 2	176	65	11	6.8
Olive Is.	2006	67	m	1150	1130	12.7	24.2	9.3	5.9 ± 3.2	28.8 ± 12.4	0.9 ± 0.7	2.2 ± 2.3	108	25	13	3.2
Olive Is.	2006	68	m	1100	1010	36	106.3	16.4	8.2 ± 4.5	23.6 ± 19	0.3 ± 0.3	3 ± 1.9	96	94	33	4.5
Olive Is.	2006	69	m	1050	1060	35.9	40.2	16.6	8.3 ± 4.5	44.8 ± 12.5	0.3 ± 0.3	3.8 ± 1.4	141	48	13	4.5
Olive Is.	2006	70	f	960	880	11.9	34.7	9.2	5.9 ± 2.6	40.9 ± 12.9	0.4 ± 0.3	3.2 ± 1.8	127	38	11	2.6
Olive Is.	2006	71	m	1420	1280	11.9	37.4	9.7	4.5 ± 2.4	41.7 ± 17.6	0.4 ± 0.4	3.4 ± 1.6	192	30	12	2.4
Olive Is.	2006	72	f	1030	1290	11.9	74.1	19	6.7 ± 3.5	32.5 ± 13.8	0.3 ± 0.3	4.9 ± 3.2	105	75	11	3.5
Olive Is.	2006	73	f	1060	1390	12	705.4	55.1	23.6 ± 8.6	25 ± 18.9	0.5 ± 0.5	3.2 ± 2.5	144	458	194	8.6

colony	year	bird #	sex	wt before g	wt after g	trip duration hrs	total distance km	max distance from colony km	mean distance from colony km ± S.D.	mean water depth m ± S.D.	mean slope of seafloor ± S.D.	mean travel speed km.h^{-1} ± S.D.	median bearing	# cells entered	# filtered track segment	sinuosity index
Reevesby Is.	2004	74	m	1160	1420	13.7	40.3	19.6	12.1 ± 5.4	18.9 ± 7.5	0.1 ± 0.1	2.4 ± 1.9	47	42	6	1.8
Reevesby Is.	2004	75	f	1040	1310	13.7	77.1	25.5	15.6 ± 6.9	20 ± 9.1	0.1 ± 0.1	6.1 ± 1.9	75	74	11	2.8
Reevesby Is.	2004	76	f		1120	13.8	60.3	14.6	8.5 ± 3.7	14.3 ± 8.1	0.1 ± 0.1	4.6 ± 2.7	54	66	12	3.8
Reevesby Is.	2004	77	m	1270	1330	13.5	65.3	19.3	10.8 ± 5.9	14.4 ± 9.2	0.1 ± 0.1	4.7 ± 2.2	70	70	13	2.7
Reevesby Is.	2004	78	m	1350	1230	10.8	78.9	27.5	6.5 ± 6.4	6.5 ± 9	0.2 ± 0.3	6.3 ± 1.6	73	79	14	2.5

Publications

The following published reports resulted from research undertaken during candidature:

Book Chapter

Johnson, G. and **Wiebkin, A.S.** (2008) Seabirds. In: Shepherd, S.A., Bryars, S., Kirkegard, I.R., Harbison, P. and Jennings, J.T. (eds). *Natural History of Gulf St Vincent.* Royal Society of South Australia, Adelaide, 324-338.

Reports

Baylis, A., Einoder, L. and **Wiebkin, A.S.** (2006). Foraging ecology of apex predators in the Great Australian Bight. Final report to Sea World Research and Rescue Foundation Inc.

Wiebkin, A.S. (2010). Little Penguins at Troubridge Island: establishing a monitoring program for the future. Final report to Nature Foundation SA incorporated. SARDI Publication Number F2010/000190-1, SARDI Research Report series No. 443.

Wiebkin, A.S. (2010). Satellite tracking Little Penguins (*Eudyptula minor*) from Kangaroo Island, South Australia. Report to the Foundation for National Parks and Wildlife.

Wiebkin, A.S. (2011). Conservation management priorities for little penguin populations in Gulf St Vincent. Report to Adelaide and Mount Lofty Ranges Natural Resources Management Board. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, SARDI Publication No. F2011/000188-1. SARDI Aquartic Sciences Report Series No. 588. 97pp.

Rogers, P., Goldsworthy, S.D., Ward, T.M., Page, B., **Wiebkin, A.** (2011). Background: Assessing the need for ecological allocations in Australia's largest small pelagic fishery. In (eds) Goldsworthy, S.D., Page, B., Rogers, P. and Ward, T (2010).

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Goldsworthy, S.D., Page, B., Rogers, P., Bulman, C., **Wiebkin, A.,** McLeay, L., Baylis, A., Braley, M., Caines, R., Huveneers, C. and Ward, T. (2011). Trophodynamics of the eastern Great Australian Bight pelagic ecosystem: implications for assessing the ecological sustainability of Australia's largest fishery. In (eds) Goldsworthy, S.D., Page, B., Rogers, P. and Ward, T. Establishing ecosystem-based management for the South Australian Sardine Fishery: developing ecological performance indicators and reference points to assess the need for ecological allocations South Australian Research and Development Institute (Aquatic Sciences), Adelaide. SARDI Publication No. F2010/000863-1. Report Series 529, 77-115.

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