Factors influencing the foraging behaviour of African Penguins (*Spheniscus demersus*) provisioning chicks at Robben Island, South Africa

by

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DECLARATION

I, Katrina (Kate) Jane Campbell, formerly Robinson, hereby declare that this thesis and the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever.

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KATRINA JANE CAMPBELL

DATE: 11 December 2016

"Courage is not the absence of fear, but the triumph over it." – Tata Nelson Rolihlahla Madiba Mandela

“She had heard it said that humans are supposed only to use about a tenth of their brains, and that no one was very clear what the other nine-tenths were for, but she had certainly never heard it suggested that they were used for storing penguins.” Douglas Adams – Long Dark Tea Time of the Soul

"My favourite image of knowledge is the old one of a candle burning on a dark night; the brighter the flame the wider the vault of the unknown behind it [...] Whatever the species, no longer need we wave goodbye to our birds on the shoreline. Now at last we have the technology to follow them to sea." Bernard Stonehouse – Penguin Biology

FOR THE PENGUINS

ABSTRACT

PhD Thesis: Factors influencing the foraging behaviour of African Penguins (*Spheniscus demersus*) provisioning chicks at Robben Island, South Africa

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Urgent and effective conservation is needed to halt the declines of endangered African Penguins. A purse-seine fisheries closure zone was in place out to 20 km around Robben Island for three years. It provided an opportunity to investigate penguin foraging behaviour in relation to estimated local prey abundance and other factors without the confounding variable of local fishing. Penguins provisioning chicks were equipped with GPS temperature depth devices for a foraging trip. Dive data (N = 75) and GPS tracks (N = 78) were collected from 78 penguins. Of those, 14 penguins were at-sea within two days of a fine-scale hydro-acoustic pelagic fish survey. Diet sampling, breeding success and chick body condition monitoring took place in the colony. Nests were followed to outcome. Morphological indicators were developed for sex determination and body condition. Intrinsic factors, brood mass, prey abundance, wave height and direction were explored in respect to foraging behaviour. Kernel density analysis identified foraging areas, confirming consistent use of the closure area. Annual differences in foraging effort were explained by variation in local prey abundance. The time the penguins spent diving and the distance travelled from the colony were negatively related to local prey abundance. There was greater variation in foraging distance when prey abundance was lower. Foraging areas and dive behaviour were similar for the sexes. The survival of chicks in the foraging study did not differ from chicks monitored in the colony for breeding success (control chicks). The trips of penguins with nesting success (N = 44) were on average 4.5 km closer to the colony than the penguins that had nesting failure (N = 21). Chick body condition in the colony was positively related to the Anchovy (*Engraulis encrasicolus*) mass percentage in the diet and the local pelagic fish abundance; condition was predicted to vary by 245% over the range of local fish abundance observed during the study period (0.5 to 187 thousand tonnes). Identifying ways to avoid depletion of prey resources around penguin colonies is important for conservation of the species.

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Chapter 1

Thesis Introduction

General introduction

Marine sentinels under threat

Seabirds are the world's most threatened bird group; they face a variety of threats from human activities on land and at sea (Croxall et al. 2012). At colonies, threats to seabirds include invasive predators (Wanless et al. 2007, Jones et al. 2008, Medina et al. 2011) and habitat change (Croxall et al. 2012). At sea, there are additional threats. Seabird health can be damaged by exposure to pollutants in the marine environment through direct exposure (Briggs et al. 1997) and bioaccumulation through the food chain (Walker 1990). Incidental oil spills (Votier et al. 2005, Barham et al. 2007) and chronic oiling (Wiese and Robertson 2004, García-Borboroglu et al. 2006) have negative demographic effects on seabird populations. Plastics move through marine food webs and affect seabird populations via direct and indirect ingestion (Ryan 1988, Derraik 2002, Cole et al. 2011). Furthermore, like other marine life, seabirds are impacted by climate change (Grémillet and Boulinier 2009, Poloczanska et al. 2013). Some seabird species face competition with fisheries for prey (Wagner and Boersma 2011, Croxall et al. 2012), gear and debris entanglements (Phillips et al. 2010, Votier et al. 2011, Wagner and Boersma 2011) as well as incidental capture as bycatch (Furness 2003, Anderson et al. 2011, Wagner and Boersma 2011, Croxall et al. 2012).

Although seabirds are a well-researched bird group, a wide range of ecological research questions remain that need to be addressed for conservation and ecosystem management purposes (Lewison et al. 2012). The following priority research questions have been outlined (Lewison et al. 2012). How are seabird spatial and temporal dynamics linked to the variability of prey and oceanographic features? What influences at sea behaviour and distributions? How do we identify key foraging areas? What is the degree to which different factors influence demographics? How can impacts of fisheries be mitigated and how do seabirds react to changing environmental and trophic factors? In addition, how do seabird behaviours influence population dynamics? Further investigation into functional relationships of seabirds to prey variability are warranted (Piatt and Sydeman 2007, Piatt et al. 2007). One of the research priorities for the conservation of seabirds in the face of global change is determining factors that affect seabird distributions and movements at sea and colony dynamics (Grémillet and Boulinier 2009).

Seabirds provide a variety of information on the marine environment; they can be used to monitor pollutant levels (Furness and Camphuysen 1997, Mallory et al. 2010, Carravieri et al. 2013), plastics (Ryan et al. 2009) and aquatic diseases (Mallory et al. 2010). Seabirds respond to changes in prey resources but care must be taken in using such responses as indicators of prey abundance (Cairns 1988, Montevecchi 1993, Furness and Camphuysen 1997, Piatt et al. 2007, Einoder 2009). Penguins in particular provide insight to ocean conditions and features (Boersma 1978, Charrassin et al. 2002, Ludynia 2007). Penguins can be considered sentinels for the marine environment (Boersma 2008, Boersma et al. 2009).

Penguins are pelagic seabirds of the order Sphenisciformes, family Spheniscidae, that are widely distributed in southern oceans from the Galapagos Islands at the equator through cool temperate waters to the polar areas of Antarctica; they are adapted to marine life but dependent on land for breeding and moulting (Stonehouse 1975, Williams 1995). Both extinct and living penguin species are considered to have adapted to underwater flight, bipedal locomotion, and feeding on small marine animals at the loss of the capacity of aerial flight during their evolution (Simpson 1975). The bio-mechanics associated with wing-propelled diving are considered to have contributed to the flightless adaptation in penguins because enhancements for this type of underwater locomotion reduce energy costs for diving but increase them for flight (Elliott et al. 2013).

Most penguin species face considerable threats. According to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, currently 15 of the world's 18 penguin species (83%) are classified as 'Near Threatened' or have an even higher risk of extinction (Table 1.1) (IUCN 2015). The African Penguin *Spheniscus demersus* is one of five penguin species classified as 'Endangered' (Table 1.1).

Table 1.1. Penguin species of the world and their IUCN Red List of threatened species status (IUCN 2015).

IUCN Status	Species	Population trend
Endangered	Northern Rockhopper Penguin *Eudyptes moseleyi*	Decreasing
Endangered	Erect-crested Penguin *Eudyptes sclateri*	Decreasing
Endangered	Yellow-eyed Penguin *Megadyptes antipodes*	Decreasing
Endangered	African Penguin *Spheniscus demersus*	Decreasing
Endangered	Galapagos Penguin *Spheniscus mendiculus*	Decreasing
Vulnerable	Humboldt Penguin *Spheniscus humboldti*	Decreasing
Vulnerable	Southern Rockhopper Penguin *Eudyptes chrysocome*	Decreasing
Vulnerable	Macaroni Penguin *Eudyptes chrysolophus*	Decreasing
Vulnerable	Fiordland Penguin *Eudyptes pachyrhnchus*	Decreasing
Vulnerable	Snares Penguin *Eudyptes robustus*	Stable
Near threatened	Gentoo Penguin *Pygoscelis papua*	Decreasing
Near threatened	Magellanic Penguin *Spheniscus magellanicus*	Decreasing
Near threatened	Royal Penguin *Eudyptes schlegeli*	Stable
Near threatened	Emperor Penguin *Aptenodytes forsteri*	Stable
Near threatened	Adélie Penguin *Pygoscelis adeliae*	Increasing
Least concern	Little Penguin *Eudyptula minor*	Decreasing
Least concern	King Penguin *Aptenodytes patagonicus*	Increasing
Least concern	Chinstrap Penguin *Pygoscelis antarcticus*	Increasing

Approach overview

Seabird predator-prey relations are integral to understanding marine ecosystem dynamics; patterns of nonlinear relations between seabird breeding success and forage fish biomass persist across ecosystems; the threshold at which breeding success declines is generally at 35% of the long-term maximum observed prey resource abundance (Cury et al. 2011). There are a variety of measures besides breeding success that can be compared with prey abundance or availability, the latter is defined as the ease with which prey are located and captured (Cairns 1988). Biological parameters can be sensitive to different time scales (Cairns 1988). For example, trip duration when provisioning for chicks can be more sensitive to changes in prey abundance than breeding success (Monaghan et al. 1994, Uttley et al. 1994, Piatt et al. 2007). There is evidence that seabird responses to their food supply are generally curvilinear but differ between species, as predicted by Cairns (1988), while thresholds to changes in prey density tend to be similar (Piatt et al. 2007). Foraging behaviour is constrained by the allometrics of body structural size and mass, that in turn influences population dynamics and food web stability (reviewed in Brose 2010). Furthermore, mobile high-order consumers can play a role in ecosystem stability (Rooney et al. 2006).

Combining biologging and hydro-acoustic technologies provides new ways of examining foraging behaviour in the context of predator-prey relations and environmental influences (Grémillet et al. 2008, Tew Kai et al. 2013). It allows researchers to study foraging behaviour at sea in relation to prey abundance. Additional information can be gained by concurrent seabird diet sampling, and chick condition and breeding monitoring. The advantages of integrating sampling of marine animal behaviour with the distribution and abundance of prey to investigate foraging ecology have been demonstrated in a number of studies of marine mammals (Boyd et al. 1994, Croll et al. 1998, Bailleul et al. 2008, Dragon et al. 2010) and seabirds (Davoren et al. 2003, Grémillet et al. 2008, Kokubun et al. 2008, Tew Kai et al. 2013). Sampling of external morphometrics contributes additional information to studies of a species' physiology and behaviour and can be relevant to understanding ecosystem change (Mallory et al. 2010).

In this thesis, I use an integrated approach to explore the foraging ecology of the African Penguin during chick-rearing by considering the concurrent data collection of: the horizontal and vertical movements of individuals at sea, measures of prey availability (abundance and distribution) from hydro-acoustic surveys, diet sampling, weather data, breeding success and measures of body condition at the Robben Island colony. To my knowledge, such a concurrent fine scale data collection is novel in the African Penguin. Predator-prey behavioural relations and the development of indicators are relevant to conservation and could provide input to ecosystem approach fisheries management.

Background information

Seabird foraging ecology

Describing the foraging ecology of seabirds involves understanding the behaviours and processes affecting feeding activity and the related spatial movements. Seabirds are generally central place foragers when raising chicks. They capture prey at sea and transport it to feed their chicks in colonies. The spatial patterning of prey in the marine environment is patchy and dynamic; however, the predictability of prey for seabirds is scale-dependent (Weimerskirch 2007). Generally, central place foraging seabirds follow behavioural modes of commuting and looping (Weimerskirch 2007) (Fig. 1.1). In a commuting mode, a bird leaves the colony on a direct path to an area where it increases its turning frequency while foraging and then returns to the colony in a generally straight and direct route; this pattern suggests predictable resources. In a looping mode, a bird makes curvilinear movements on the outward path and typically returns to the colony from a different direction from the outward path; this pattern suggests food resources are less predictable (Weimerskirch 2007) (Fig. 1.1). These patterns differ from correlated random search modes, where the animal moves in successive random directions, which is rarely seen in seabirds (Weimerskirch 2007) (Fig. 1.1).

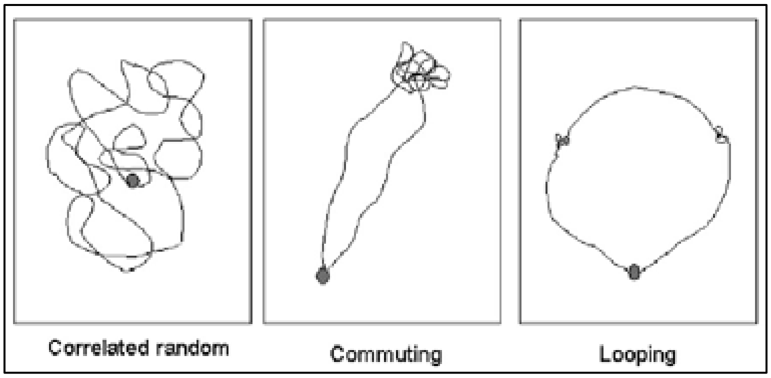

Figure 1.1. Types of movements of a central place forager, reproduced with permission from Weimerskirch (2007). The grey circle indicates the location of a colony while the line indicates a typical foraging track expected for three broad types of behaviour.

Game and optimal foraging theory are often used to explain animal behaviour and predator-prey relations. Game theory provides the view that the success of a strategy or decision depends on what others are doing. In this way, it gives explanations for group behaviours such as schooling where each animal tries to reduce its chance of being caught by a predator (Hamilton 1971). It can also be applied to seabird-prey spatial interactions which can be explained as two-way games where seabirds are seeking out concentrations of prey, which are moving to avoid predation, and both are acting within their own spatial constraints (Fauchald 2009). Optimal foraging theory predicts that feeding animals behave in a way to maximise their fitness (Schoener 1971, Pyke 1984, Parker and Smith 1990).

Questions of optimisation can be investigated in terms of foraging (Weimerskirch et al. 2000, Boersma et al. 2009, Watanabe et al. 2014, Ford et al. 2015) and dive behaviour (Mori 2002, Mori et al. 2002, Halsey 2003). The marginal value theorem is an extension of optimal foraging theory that provides mathematical models of how animals should spend their time foraging when food resources are in patches (Charnov 1976). There is observational support that penguins follow the behavioural predictions from marginal value theorem (Watanabe et al. 2014). Yet, the assumptions of these types of theories are not always met in penguins because they have been observed foraging as soon as they leave the colony so they do not always forage in discrete patches (Ford et al. 2015) and penguins do not necessarily meander more following a long trip than after a short trip to identify closer prey patches. Rather, it appears they return to previously visited locations sometimes switching between near and far (Boersma et al. 2009, Saraux et al. 2011). These theories provide ways to think about how seabirds make decisions and interact with their prey.

Regime shifts and global climate change can cause match/mismatch between the timing and spatial location of food resources (Durant et al. 2007, Grémillet and Boulinier 2009). To predict how trophic changes impact predator-prey relationships and whether seabirds will be able to adapt to trophic or environmental change requires an understanding of foraging behaviour plasticity, influences of environmental and intrinsic factors, and the relationships to population dynamics. For these reasons, research needs to be conducted both at sea and on land, and in combination (Grémillet and Boulinier 2009).

Advances in technology, analysis and conceptualisation

Advancements in device technology have expanded opportunities to examine animal behaviour in the marine environment (Kooyman 2004, Wilson et al. 2007, Rutz and Hays 2009). Tracking marine vertebrates can provide information to inform species conservation (Schofield et al. 2007, Burger and Shaffer 2008, Bograd et al. 2010, Montevecchi et al. 2012, Thaxter et al. 2012) and in some cases about population dynamics (Morales et al. 2010).

There are an increasing number of ways in which animal movement can be analysed (Lewison et al. 2012). There has been progress in modelling complex behaviour that incorporates spatial constraints, observational error, and biological-based processes (Schick et al. 2008). Several analytical methods are available to identify seabird foraging areas such as kernel density, first time passage and state-space analysis (Lewison et al. 2012, Tancell et al. 2013). These advances have stimulated the conceptualisation of movement ecology as a growing discipline (Nathan et al. 2008). Recently, fractal analysis has been applied to penguin behavioural investigations (e.g., Meyer et al. 2015, Reynolds et al. 2015).

Southern Benguela ecosystem and range shifts of pelagic fish

The Benguela is an eastern boundary oceanic upwelling system, located on the south west side of Africa; its highly dynamic oceanographic and biotic features have been described (van der Lingen et al. 2006b, Hutchings et al. 2009). It is divided into two sections at Lüderitz upwelling cell at 26°S: the northern and southern Benguela. The southern Benguela is generally taken to extend south from 26°S to the Agulhas Bank bounded by the Agulhas Current (Shannon 2006, van der Lingen et al. 2006b, Hutchings et al. 2009). Regime shifts in the southern Benguela have occurred (Blamey et al. 2012, 2015) but not to the extent observed in the northern Benguela where the declines in foraging fish and environmental perturbations have been greater (Cury and Shannon 2004).

The main oceanographic components of the southern Benguela are the coastal upwelling and the meeting of cold waters from the South Atlantic and Southern Ocean and the warm water from the Agulhas Current (Figure 1 of Shannon 2006). Wind patterns drive the coastal upwelling in the southern Benguela (Andrews and Hutchings 1980). The anti-clockwise South Atlantic high pressure system shifts seasonally creating annual rainfall and wind patterns (Hutchings et al. 2009). The Benguela Upwelling system generates generally northward movement of surface water along the west coast of South Africa; the thermal difference between cold upwelled water and the cold South Atlantic water meeting the warm Agulhas Current creates eddies and jet currents that flow northward influencing the life-cycle of pelagic fish (Hutchings 1992, Hutchings et al. 2009).

The southern Benguela is a nursery ground for several fish species that spawn on the Agulhas Bank because a jet stream transports the eggs and larvae northward into this area (Hutchings et al. 1998, 2002, 2009). The young of the year, the recruits, then swim southward to return to the spawning areas on the Agulhas Bank (Hutchings et al. 1998, 2002, 2009). Small pelagic fish are particularly important in such ecosystems because of their ecological role at an intermediate trophic level (Cury et al. 2000). Variability in upwelling ultimately results in variable phytoplankton concentrations along the South African west coast (Hutchings et al. 2009), which can impact species abundance, trophic structure and community assemblages in the Benguela (van der Lingen et al. 2006b). Sardines (*Sardinops sagax*) and Anchovy (*Engraulis encrasicolus*) have similar life histories but distinct trophic differences in zooplankton feeding preferences (van der Lingen et al. 2006a). Overlap of Anchovy and Sardine is mainly restricted to a coastal band at depths less than 150 m (Drapeau et al. 2004). Juvenile Anchovy and

Sardine aggregate inshore along the South African west coast and shoal together (van der Lingen et al. 2006a).

Anchovy and Sardine are not only ecologically important but also have an economic value as target species of the purse-seine fishing industry, contributing over 75% of the total pelagic catches in the southern Benguela (van der Lingen et al. 2006a). The dominance of Anchovy or Sardine in fishery catch has alternated over time in the southern Benguela (van der Lingen et al. 2006a, Blamey et al. 2015). Sardine was initially the target species but annual catches declined over the late 1960s and changes in mesh sizes allowed for catches to diversify to Anchovy (van der Lingen et al. 2006a, Jarre et al. 2013). Anchovy was targeted because it became the more dominant species (Jarre et al. 2013). There was an increase in the abundance of both species in the early 2000s followed by decreases in Sardine and to a lesser extent Anchovy in the mid-2000s; Anchovy remained the dominant species with larger spawning populations and greater recruitment (Coetzee et al. 2008).

Environmental temperature changes led to eastward shifts in spawner distributions of Anchovy (Roy et al. 2007) and Sardine (van der Lingen et al. 2005) along the Agulhas Bank in the mid-1990s; these persisted to at least 2014 (Blamey et al. 2015). In spite of the eastward shift in spawning distribution, the transport of eggs and larvae from these eastern spawning areas is still predominantly to the west coast of South Africa for both Anchovy (Roy et al. 2007) and Sardine (van der Lingen et al. 2005). However, the eastern distribution shifts of adult Anchovy and Sardine have had rippling effects up the food chain for African Penguins (Crawford 1998, Crawford et al. 2008) and other seabirds such as Cape Gannets (*Morus capensis*), Cape Cormorants (*Phalacrocorax capensis*) and Swift Tern (*Sterna bergii*) (Crawford 1998, van der Lingen et al. 2005, 2006b, Crawford et al. 2008, 2014) and for the purse-seine fishing industry (van der Lingen et al. 2005, Jarre et al. 2013).

The recruitment and spawning of these species are monitored by large scale hydro-acoustic surveys by the South African government's Department of Agriculture, Forestry and Fisheries (DAFF, Hampton 1987, Coetzee et al. 2008). Considerable research has addressed the prediction and modelling of recruitment, spawning and transport for Anchovy (Painting et al. 1998, Hutchings et al. 1998, Mullon et al. 2002, 2003, Huggett et al. 2003, Parada et al. 2003).

Changes have been observed in catch abundance and the distribution other pelagic species such as Cape Horse Mackerel (*Trachurus capensis*), although the changes in Cape Horse Mackerel have been attributed largely to fishing pressure on the west coast (Griffiths et al. 2004, van der Lingen et al.

2006b). Juvenile Cape Horse Mackerel shoal with Anchovy and Sardine (Griffiths et al. 2004) but their life-cycle is more complex (Barange et al. 1998, Hutchings et al. 2002). Cape Horse Mackerel are thought to be near-surface pelagic as juveniles and then become demersal, settling over the shelf break at older ages and rising again in the water column during migration and spawning periods (Barange et al. 1998). Bottom trawl surveys on the west coast indicate that juvenile Cape Horse Mackerel concentrate at the shelf break along the 200 m isobar (Barange et al. 1998). Cape Horse Mackerel made up portions of South Africa's west coast pelagic fishery catch from 1950 to 1965 but since the 1970s adults have not been present in catches on the west coast (van der Lingen et al. 2006b). Acoustic and midwater trawl surveys from 1984 to 1996 indicated Cape Horse Mackerel of length > 30 cm were only found east of Cape Agulhas (Barange et al. 1998).

A recent re-evaluation of the adult distribution in the southern Benguela using data from acoustic surveys (1997–2007), mid-water trawl (1997–2010) and demersal trawl (1984–2011) showed the majority of the adult population remains on the south coast with a small adult population at St. Helena Bay (Mc Laverty 2012). The juvenile Cape Horse Mackerel, on the other hand, have remained present in west coast catches in small numbers (< 10,000 t), except in 2011 when there was an unusually large catch of 12,000 t (van der Lingen et al. 2006b, van der Lingen pers. comm.). The majority of juvenile Cape Horse Mackerel recruitment remained on the west coast from 1997 to 2010, although there is an increasing occurrence of recruits on the south coast (Mc Laverty 2012).

Abiotic factors play a key role in the Benguela variability (Hutchings et al. 2009). Changes to dynamic systems such as the southern Benguela ecosystem can have multiple drivers which can be difficult to disentangle (Blamey et al. 2015). Pelagic fishing pressure has been a component of southern Benguela ecosystem change since the 1950s (Hutchings et al. 2012, Jarre et al. 2013) and an inter-connectivity exists between the biological and social drivers of historical changes that have occurred (Jarre et al. 2013).

The study species: African Penguin

Species' description

The African Penguin was previously known as Jackass Penguin and Black-footed Penguin. Adults have black upperparts and white underparts similar to other *Spheniscus* species, but they have a single black breast band and usually no bands on the white throat (Fig. 1.2). They have pink exposed skin at the base of the bill and encircling their eyes. The bill is black with a lateral grey stripe at the nostrils. Adult

African Penguins have unique plumage spot patterns which can be used for individual identification because the patterns remain stable for life (Sherley et al. 2010). Immature birds are grey brown and some undergo partial moult to adult plumage (Fig. 1.2). The African Penguin distribution range is around the coastal areas of Namibia and South Africa with most colonies on coastal islands (Crawford et al. 2011) (Fig. 1.3).

Figure 1.2. African Penguin adults with black and white plumage and immatures with grey and white plumage on the Robben Island shoreline. Photo courtesy of Leanne Tol.

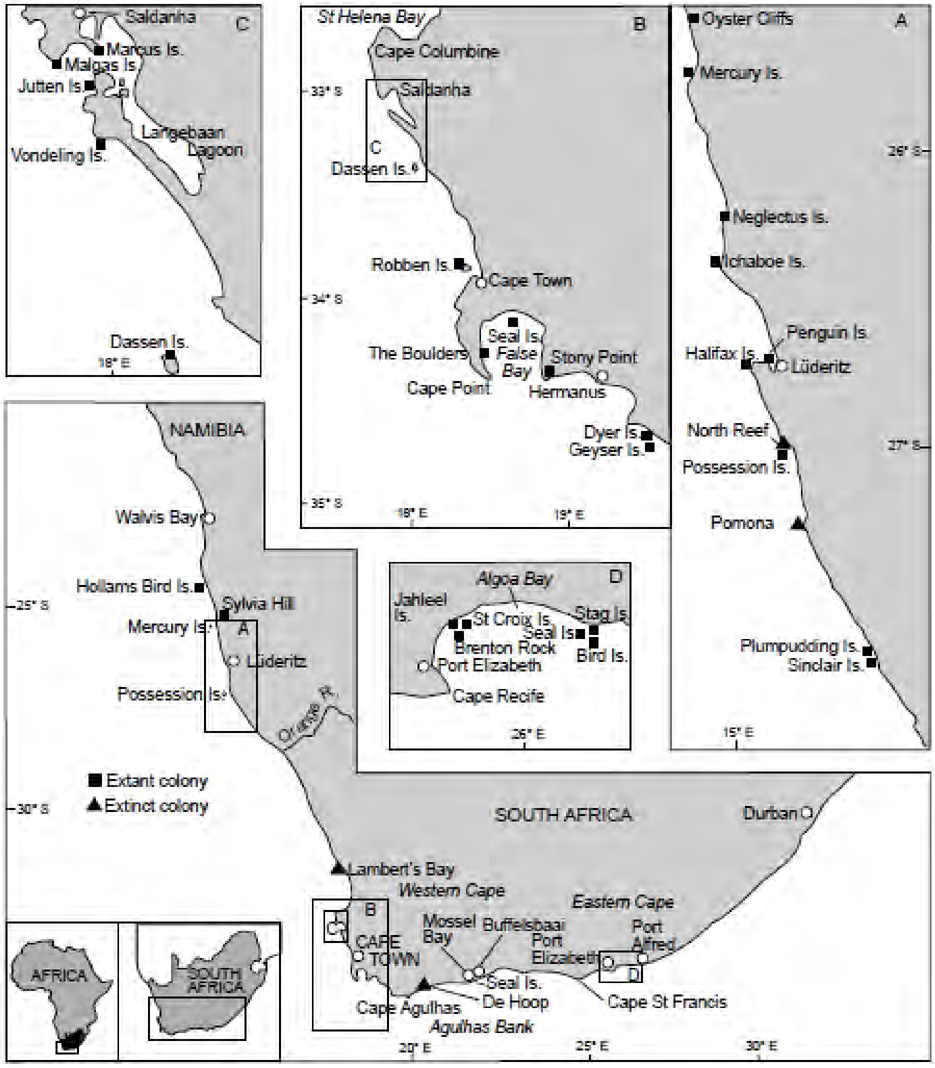

Figure 1.3. Breeding localities of extant and extinct African Penguin colonies 1990–2010, reproduced with permission from Crawford et al. (2011). The Robben Island colony is situated in section B.

Conservation status, threats and protection

The African Penguin fulfils the IUCN Red List status of 'Endangered' by direct observation of decreases of greater or equal to 50% of the number of total individuals over the last three generations and projected to occur within the next three generations due to declines in area of occupancy, habitat quality, impacts from introduced taxa, competitors and pollutants (BirdLife International 2013). The South African breeding population decreased by 70% from an estimated 56,000 breeding pairs in 2001, to 17,000 breeding pairs in 2013 (Crawford et al. 2011, 2014). Over the period of this study, from 2011 to 2013, the number estimated to be at the Robben Island colony decreased by 24.9% from 1,817 to 1,364 breeding pairs (Department of Environmental Affairs, unpublished data).

The African Penguin has been impacted by a multiple threats, both historical and current. Historical causes of the species' decreases are changes to habitat from guano collections which took place at South African islands from 1843 to 1994 (Griffiths et al. 2004), a long history of egg harvesting which was authorised as a commercial food source until 1968 (Shelton et al. 1984, Griffiths et al. 2004), and oil spills (Underhill et al. 1999, Crawford et al. 2000, Barham et al. 2007, Wolfaardt et al. 2009c). Chronic oiling continues to be a threat (Parsons and Underhill 2005). There is competition for prey resources between African Penguins and pelagic fisheries (Frost et al. 1976, Crawford 2007, Pichegru et al. 2009); foraging ranges of breeding African Penguins in South Africa overlap with areas of pelagic fisheries catches (Pichegru et al. 2009). The eastward shift of Sardine and Anchovy is thought to have further compounded food shortages for the African Penguin (Crawford 1998, 2007, Crawford et al. 2014). The proportion of South Africa's population that bred in the Western Cape was 81% in 2005, but from 2011 to 2013, fell to less than 50% (Crawford et al. 2014).

Long-term mitigation of direct competition with pelagic fisheries requires the integration of functional and spatial relationships between penguins and fish stocks into an ecosystems approach to fisheries management (Shannon et al. 2006, Crawford 2007, Sherley et al. 2013b). One approach toward limiting the impacts of fisheries on seabird colonies that can have rapid benefits for penguins is the implementation of pelagic fisheries closure areas around African Penguin colonies (Pichegru et al. 2010). However, the closure scale of area and changes in fisheries catch need to be taken into account for there to be improvements in food availability for penguins (Pichegru et al. 2012, Sherley et al. 2015).

The African Penguin is protected under South African legislation and a biodiversity management plan (BMP) which lists the research priority areas (Government Gazette of South Africa 2013). Investigations into foraging behaviour and population dynamics are included in the research priorities listed for the species. Exploring the links between provisioning foraging effort, prey abundance, diet composition and chick body condition will contribute towards capacity for integrated population modelling of African Penguin demographics. This thesis contributes to those research objectives.

Some African Penguin colonies are within Marine Protected Areas (MPAs). The Namibian Islands Marine Protected Area (NIMPA) places restrictions on fishing, mining, underwater explosions, guano scraping, mariculture and boat-based tourism with prohibitions on purse-seining in the buffer zone within which African Penguin colonies are found (Government Gazette of the Republic of Namibia 2009, 2012). The area adequately encompasses the African Penguin’s key foraging areas (Ludynia et al. 2012a). In South Africa, MPAs have been established around penguin colonies at Jutten Island, Malgas Island, Betty's Bay (Stony Point colony) and Table Mountain (Boulders colony), and Bird Island (Wood 2007) (Fig. 1.3). Of those, Table Mountain MPA and Bird Island Group have no-take zone sections (Wood 2007). The Boulders colony is within a fisheries no-take zone called The Boulders Sanctuary Zone in which all forms of fishing are prohibited (Government Gazette of South Africa 2004). The Bird Island Group is an MPA designated in 1998 around Bird Island in the Eastern Cape with a fisheries no-take area of 70.4 km^2 (Wood 2007). As of 2015, there was no MPAs around the African Penguin colonies of Robben and Dassen Islands in Western Cape or St. Croix Island in the Eastern Cape. In 2016, a Robben Island Marine Protected Area was gazetted and the Robben Island Marine Protected Area Regulations, which restricts fishing in Robben Island Controlled Zones (RICZ) and prohibits it in the Robben Island Restricted Zone (RIRZ), commenced upon the date of publication that called for comments (Government Gazette of South Africa 2016).

The efficacy of purse-seine fishery closures around African Penguin colonies is being investigated by DAFF’s Small Pelagic Scientific Working Group since 2008 (Cherry 2014). There is evidence that the closure at Robben Island improved chick survival by 18% (Sherley et al. 2015). Evaluating the effectiveness of such an approach at a Western Cape colony is beyond the scope of this thesis. However, a detailed investigation of the African Penguin’s provisioning behaviour and breeding at Robben Island while a purse-seine fishing closure out to a 20 km radius around the island was in effect can contribute to our understanding of the underlying dynamics and assist the determination of effective conservation measures.

Life history

African Penguin life history parameters and threats have been reviewed in detail at a species level (Crawford et al. 2013) as well as at a colony level for Robben Island (Weller et al. 2014) and Dyer Island (Ludynia et al. 2014). Life history is briefly provided below as background information on the species and details pertinent to the Robben Island study site.

Moult

Once a year adult African Penguins replace all their feathers to maintain their insulation from the cold seawater, a physiological process called moult (Randall 1989). It is necessary for survival and requires sufficient energy reserves. In the pre-moult phase African Penguins increase their mass by ca. 30% (Randall 1989). During moult, African Penguins remain ashore, do not feed and display little activity besides preening while they replace their entire plumage (Cooper 1978). The duration of moult is approximately 21 days; at the completion of moult they have had a mass loss of ca. 46% from the start of moult, which is followed by a period of feeding at sea (Randall et al. 1986). So overall, after moult they have had a mass loss of c. 16% of their mass prior to the pre-moult fattening. Moult tends to be more synchronised than breeding (Wolfaardt et al. 2009b). However, the extent of the synchronicity can differ between colonies (Wolfaardt et al. 2009a) and the timing of moult varies at different localities (Crawford et al. 2013). At the Robben Island colony, moult takes place between November and January (Crawford et al. 1995, Underhill and Crawford 1999). Adult moult is more synchronous than that of immatures (Wolfaardt et al. 2009a). Immatures moult to adult plumage at 12 to 22 months old (Randall 1989) after which they follow the annual adult moult cycle (Wolfaardt et al. 2009a). The subadults spend most of their time at sea until they reach breeding maturity (Randall 1989).

Breeding biology

African Penguins begin breeding successfully typically at four to six years old (Whittington et al. 2005), but individuals have been recorded as attempting to breed as young as at one year and eight months old (Crawford et al. 1999). At Robben Island, most six year-old adults have bred for the first time (Whittington et al. 2005). The species has strong site fidelity to the colony in which they first breed (Crawford et al. 1995, 2013) and strong mate fidelity has also been observed (Crawford et al. 1995). Parental care is shared both during incubation and chick rearing. When chicks are small, adults alternate chick guarding and foraging trips on a daily basis (van Heezik and Seddon 1996).

At the Robben Island colony, the African Penguin breeding period begins in January and ends in early November; peak egg-laying occurs from February to April, and small downy chicks are abundant from April to September (Crawford et al. 1995). Breeding corresponds to times when young Anchovy and Sardine are migrating past the island southwards to the Agulhas Bank (Crawford et al. 2006). The African Penguin is a burrow nester but can nest in the open, under vegetation and in a variety of nest types including artificial burrows and nest boxes (Kemper et al. 2007, Pichegru 2012, Sherley et al. 2012).

In general, clutches contain two eggs, sometimes one egg and on rare occasions three (Crawford et al. 1999, 2013, Kemper 2006). There is an average hatching asynchrony of 2.3 days; the A-chick is on average 41% heavier than the B chick (van Heezik and Seddon 1996). This asynchrony is thought to allow more efficient resource allocation as satiation in the A-chick ensures a compromise between their direct and indirect fitness (van Heezik and Seddon 1996). Chicks can be classified into five stages – P0 to P4 (Barham et al. 2007). Chicks at hatching (P0) are grey downy and do not have eyes that are open (Seddon and van Heezik 1993) (Fig. 1.4A). Small downy chicks with eyes open being brooded by adults are at P1 stage (Fig. 1.4B). At around 16 days old chicks sit up and develop white downy plumage on underparts (Seddon and van Heezik 1993); these small chicks are at P2 stage (Fig. 1.4C). At the P3 stage chicks are large, more than three-quarters of adult size; down around the face and possibly elsewhere starts to be lost (Fig. 1.4D). Most African Penguin chicks begin to lose their down by 40 days old (Seddon and van Heezik 1993). Chicks obtain juvenile blue-grey plumage as early as 61 days old (Seddon and van Heezik 1993); this is P4 stage (Fig. 1.4E). For further details on chick developmental stages see the supplementary materials in Sherley et al. (2014). Parental care of chicks can be divided into two phases: guard and post-guard (Cooper 1977, Seddon and van Heezik 1993). Chicks are first left unguarded when about 26–30 days old (Seddon and van Heezik 1993). At Robben Island, African Penguins can lay second clutches but third clutches during a breeding season are rare (Crawford et al. 1999).

Figure 1.4. African Penguin chicks stages: (A) one P0 chick next to an egg being brooded by an adult, (B) one P1 chick being brooded by adult, its head is visible left of the adult's wing, (C) two P2 chicks being brooded by adult, (D) one P3 chick next to an adult, (E) two P4 chicks. Photo (A) is courtesy of Elsa Bussière.

Prey

The main prey of African Penguins is pelagic fish: Anchovy and Sardine (Crawford 2007, Crawford et al. 2014). At Robben Island, diet samples collected from 1989 to 2009 from breeding penguins, showed that young of the year Anchovy contributed 84% of prey mass on average and Sardine contributed 3% (Crawford et al. 2011, Sherley et al. 2013b). Cape Horse Mackerel contributed 4% on average over those years (Sherley et al. 2013b). The other prey species[1] each contributed less than 3% of prey mass on average (Sherley et al. 2013b).

Foraging behaviour

The first types of 24-hour data-loggers were depth gauges and speed meters pioneered on the African Penguin (Wilson and Bain 1984a, 1984b, Kooyman 2004). Since then, a body of knowledge has been collected on the foraging behaviour of chick-rearing African Penguins in the southern Benguela (Wilson 1985a, 1985b, Wilson and Wilson 1990, Petersen et al. 2006, Pichegru et al. 2009, Waller 2011), in the Eastern Cape near the Agulhas Current (Pichegru et al. 2009, 2012, 2013, Wright et al. 2011, van Eeden 2012) and in Namibia in the Northern Benguela Current (Ludynia 2007, Ludynia et al. 2012b). Recently, research has extended to juvenile movements (Sherley et al. 2013a) and those of adults outside of the breeding season (Harding 2013). The dive behaviour of African Penguins is well described (Wilson and Wilson 1995) and is similar to that of other *Spheniscus* penguins (Ryan et al. 2007). At Robben Island the average and maximum dive depths are 17.8 m and 62.9 m, respectively; the dive duration average and maximum are 51 seconds and 142 seconds, respecitvely (Ryan et al. 2007).

Like other seabirds, African Penguins are central place foragers when raising chicks. This restricts the foraging range of African Penguins. At Robben and Dassen Island birds have been observed to have an average foraging range of 9.4 km and the farthest distance was 16.8 km (Petersen et al. 2006). Greater maximum foraging range distances have been recorded at Dyer Island of up to 52.1 km

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[1] Round Herring (*Etrumeus whiteheadi*), Squid (Loligo *spp.*), Beaked Sandfish (*Gonorynchus goborynchus*), Cape Hake (*Merluccius capensis*), Gurnard (Chelidonichthys spp.), Mantis Shrimp (*Pterygosquilla armata capensis*), Longsnout Pipefish (*Syngnathus acus*), Silvery Lightfish (*Maurolicus muelleri*), Snoek (*Thyrsites atun*), Buttersnoek (*Lepidopus caudatus*), Southern Mullet (*Liza richardsonii*), West Coast Rock Lobster(*Jasus lalandii*), Chub Mackerel (*Scomber japonicus*), Atlantic Saury (*Scomberesox saurus*), Cape Sandlance (*Gymnammodytes capensis*), Goby (Gobiidae spp.) and Slender Snipe Eel (*Nemichthys scolopaceus*)

(Waller 2011), 27.9 km at mainland colonies (Petersen et al. 2006), 44.5 km at East Coast colonies (Pichegru et al. 2012) and 31.9 km in Namibia (Ludynia 2007, Ludynia et al. 2012b). African Penguins generally forage during the day (Wilson and Wilson 1990, Wilson et al. 1993, Petersen et al. 2006, Ludynia 2007, Ryan et al. 2007, Waller 2011). They have been observed to forage as singletons as well as in small groups and in large coordinated groups (Wilson et al. 1986, Ryan et al. 2012). Group sizes up to 12 dive synchronously (Wilson et al. 1986). The location of bite marks on prey provide evidence prey capture occurs from below (Wilson and Duffy 1986, Wilson and Wilson 1990). African Penguin foraging behaviour is well-documented (Wilson 1985a, Wilson and Wilson 1995, Ryan et al. 2012, Crawford et al. 2013), particularly while breeding (Wilson 1985b, Wilson and Wilson 1990, Ludynia 2007, Pichegru et al. 2009, 2012, 2013). However, questions remain such as, 'how variable is provisioning foraging over the breeding season?', 'What extrinsic factors influence the foraging behaviour of African Penguins and to what extent?, 'Does the prey abundance around the colony influence the body condition of chicks?' and 'Can foraging behaviour be an indicator of breeding success?'

Study site: Robben Island colony

Colony description

Robben Island (33°48’S, 18°22’E) is a UNESCO World Heritage Site and an Important Bird Area in Table Bay, 10 km north-west of Cape Town harbour. Its area is 5 km^2. The western side of the island is exposed to the open ocean and has more wave action than the eastern side. The currents in Table Bay are mainly wind driven with weak velocities of ca 0.2 m/s. When southerly winds prevail, the current is generally northward and creates an anti-clockwise pattern around the island; north-westerly winds reverse currents to clockwise (Rossouw et al. 2000). Robben Island, as part of the Western Cape province of South Africa, has a Mediterranean climate. Mean monthly temperatures range from 8°C to 23°C; austral summers (November to February) are hot and dry, and winters (May to August) are cool and wet with ca. 60% of the annual rainfall occurring in these four months (Rossouw et al. 2000). The island’s terrestrial ecology has been impacted by human habitation of the island since the 1650s, changes in land use and the introduction of species such as Feral Cats (*Felis catus*), Europeun Rabbits (*Oryctolagus cuniculus)* and European Fallow Deer (Dama dama) (Adamson 1934, Crawford and Dyer 2000, Rossouw et al. 2000, de Villiers et al. 2010, Sherley 2010, Sherley et al. 2011). Since 1996 the island has been a government-run museum (Rossouw et al. 2000).

The vegetation on the island can be divided into three main categories: dense strands of bush interspersed with trees, grasslands, and plantations of alien gum trees (Eucalyptus spp.) and Pine(*Pinus pinaster*) trees (Crawford et al. 1995). Penguins nest in areas of introduced Rooikrans (*Acacia cyclops*), Manatoka (*Myoporum serratum*), Pine and gum trees (Crawford et al. 1995). Robben Island is dominated by sandy soils (Adamson 1934, Rossouw et al. 2000), making burrows susceptible to collapse (Sherley et al. 2012). The most common nest type are open scrape nests under vegetation but penguins also nest in derelict buildings, under man-made structures, in wooden nest boxes and artificial burrows made of fibre glass and covered with soil (Sherley et al. 2012).

Colony history

There are records of African Penguins breeding at Robben Island from 1620 to 1727, after which they were absent from the island for approximately two centuries (Crawford et al. 1995). The island was recolonised in 1983 (Shelton et al. 1984). Although penguins were released on the island from a rehabilitation centre prior to the recolonisation, flipper-band evidence indicates birds emigrated from Stony Point and Dyer Island to Robben Island (Crawford et al. 1995). Explanations for the recolonisation of Robben Island include available breeding habitat, food availability, regular presence of other seabirds, and the lack of breeding fur seals (Crawford et al. 1995). The number of breeding pairs increased to a maximum in 2004 and subsequently decreased rapidly (Fig. 1.5). Long-term monitoring has taken place at this colony; a census of active nest sites has taken place annually since 1984 and counts of moulting birds at 14 day intervals (Randall et al. 1986) since 1988 (Crawford et al. 1995). Monitoring of breeding success has been conducted in the same way since 2001 (Crawford et al. 2006, Barham et al. 2007, Sherley et al. 2013b). Diet sampling of breeding birds started in 1989 (Crawford et al. 2011). Population dynamics have been studied in detail at Robben Island (Crawford et al. 1999, Weller et al. 2014).

Predators at Robben Island

African Penguins have terrestrial and marine predators at the Robben Island colony (Weller et al. 2014). Mole Snakes (*Pseudaspis cana*) (Underhill et al. 2010) and Kelp Gulls (*Larus dominicanus*) (Sherley et al. 2012) eat eggs while Feral Cats eat eggs and chicks up to P3 stage (Crawford et al. 1995, Sherley et al. 2012). There is a cat eradication programme in place (de Villiers et al. 2010). At sea, potential predators around Robben Island are Cape Fur Seals (*Arctocephalus pusillus pusillus*) (David et al. 2003) and Great White Sharks (*Carcharodon carcharias*) (Weller et al. 2014); there has been evidence of such predation at Dyer Island (Johnson et al. 2006) which is < 200 km away from Robben Island by sea.

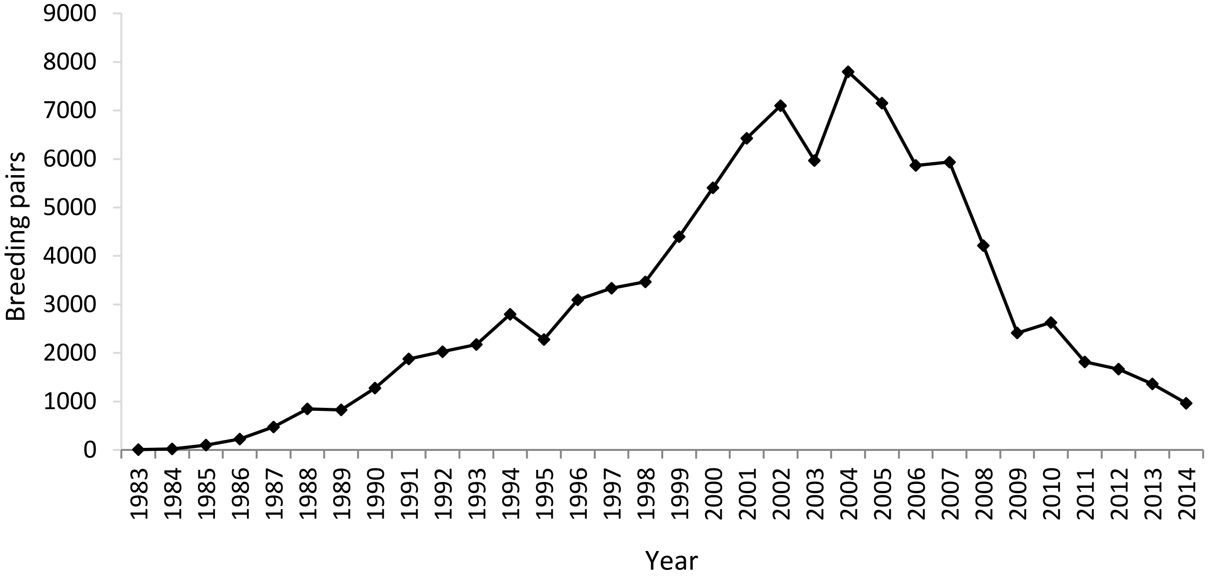

Figure 1.5. Numbers of breeding pairs of African Penguin on Robben Island from 1983 to 2014 from annual census conducted by the Department of Environmental Affairs, South Africa (DEA, unpublished data).

Conservation efforts at Robben Island

At Robben Island, artificial nests are in place and there is evidence that they improve chick survival (Sherley et al. 2012). Chick bolstering occurs, whereby searches for abandoned chicks take place in November and those chicks are then raised in captivity at SANCCOB (Southern African Foundation for the Conservation of Coastal Birds) and released to the wild where they survive and recruit into breeding populations at similar rates to their wild counterparts (Sherley et al. 2014).

Study rationale

A closure of purse-seine fisheries was in place out to an extent of 20 km radius around Robben Island for the three years of this study (Sherley et al. 2015). Fine scale hydro-acoustic surveys for pelagic fish were conducted around the island during that time (Merkle et al. 2009, 2012a, 2012b). This provided a unique opportunity to investigate African Penguin foraging behaviour in relation to prey abundance and distribution. Behavioural research in relation to individual body condition and population dynamics is needed for a holistic understanding of the species.

Animal ethics and implications for methodology

Animal ethics require careful consideration of the potential research impacts on the study species and their offspring; mitigation of impacts is especially important when devices are attached to study animals (Hawkins 2004, Wilson and McMahon 2006). Research that collects data from animals by attaching data logging devices is termed biologging. These types of studies with species at risk can provide useful information for species' conservation but the research must not contribute to the species' decline or hinder recovery rates (Cooke 2008). Therefore, particularly when researching an endangered species, researchers need to be aware of their impacts. The wellbeing of the study species was always prioritised. Birds were carefully selected to be equipped with a device for one foraging trip. Deployments were restricted to one adult of a nesting pair and only once per adult penguin.

Thesis aims and outline

The main aim of this research project was to investigate the foraging behaviour of breeding African Penguins at a colony in the southern Benguela in relation to the local prey abundance and other intrinsic and extrinsic factors. To do this, morphological indicators were further developed for sex determination and body condition indices.

Chapter 1 provides an introduction to the thesis with background information, study rational, implications of animal ethics for methodology as well as the thesis aims and outline.

Chapter 2 explores methods of sexing of African Penguins by bill morphology. It presents a simple discriminant function method, compares it with other existing methods and assesses whether such a method is applicable throughout the species' South African range.

Chapter 3 presents an African Penguin adult body condition index using quantile regression techniques and outlines how it can be a useful tool for rehabilitation centres and research. It also addresses the contribution of prey load and makes suggestions for effective sampling methods.

Chapter 4 contains an investigation of the inter- and intra-annual variation in foraging behaviour of African Penguins provisioning small chicks at Robben Island. Dive behaviour, prey pursuits and core foraging areas are explored in detail. The chapter also assesses whether bird structural size, body mass, body condition index, chick mass or wave conditions influence foraging behaviour.

Chapter 5 combines fine-scale pelagic fish surveys with African Penguin tracking to explore penguin foraging behaviour relative to local prey distribution and abundance. Comparing the distributions of African Penguins to the distributions of their pelagic prey at different scales is beyond the scope of this thesis. However, examining pelagic fish distributions at fine scales when African Penguins were at sea with devices provides the opportunity to address whether breeding African Penguin behaviour changes in response to changes in pelagic fish abundance around a colony.

Chapter 6 presents an extension of the chick body condition index for small sized chicks and compares chick body condition in the colony to the pelagic fish abundance and diet composition. It also compares chick body condition to the foraging effort of a parent and the parental body condition.

Chapter 7 investigates whether survival of chicks in the foraging study differed from that of those monitored in the colony for breeding success. It also raises the question of whether parental foraging distance could be used as an indicator of breeding success.

Chapter 8 presents the overarching links of this thesis and the main conclusions. It makes suggestions for future research directions.

This thesis provides a fine-scale investigation of penguin foraging behaviour in relation to local prey availability and other factors. It explores the relationships between provisioning foraging behaviour, prey abundance, diet composition and chick body condition. The thesis identifies core foraging areas of penguins breeding at the Robben Island colony and contributes to the African Penguin BMP priority research.

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Chapter 2

Sexing African Penguins using bill measurements: method comparisons and implications for use

The content of this chapter is a paper published in Ostrich for which I am first author. It is entitled 'Sex Determination of African Penguins (*Spheniscus demersus*) using bill measurements: method comparisons and implications for use' by Campbell, K. J., Farah, D., Collins, S., Parsons, N. It was written in collaboration with Dani Farah, Sarah Collins and Nola Parsons. We all contributed to the direction, analysis, scope and writing of this chapter. Dani Farah devised the Farah discriminant function presented. I conducted most of the subsequent analysis and prepared the paper for publication under the oversight of Nola Parson and input from co-authors. The text has been left in the original plural voice to reflect the collaborative nature of this chapter.

African Penguins are sexually dimorphic; on average males are larger than females but measurements overlap often making sex determination difficult through observations alone. This chapter presents a simple discriminant function using bill length and depth from a sample of birds sexed from gonad visualization during post-mortem analysis and compare it with other existing methods. It correctly assigned 90% of molecularly sexed birds and 91% of birds sexed by partner measurement comparisons. The use of discriminant function score cutpoints, while leaving 16% and 29% of birds as unclassified, improved classification accuracy of those groups to 97% and 99%, respectively. Bill depth was found to be a discriminating variable. However, two techniques for measuring bill depth are currently in use for this penguin species. While these measurements are correlated (*r* = 0.85) they differ on average by 1.4 mm hindering sex determination accuracy when using a discriminant function developed from the other bill depth measurement. Exploration of adult bill morphology of DNA-sexed birds at different colonies and regions indicates these methods are widely applicable throughout the African Penguins' South African range.

Introduction

In bird species with little or no external sexual dimorphic features, sexing methods are especially important for field research. Identifying adult sex ratios in wild bird populations can assist with the understanding of population dynamics, habitat use, survival and behavioural patterns (Donald 2007). Non-invasive sexing techniques for the African Penguin need to be checked for reliability and the scope of geographical variation of bill morphology needs to be assessed for effective implementation in the field.

A variety of sexing techniques exist in *Spheniscus* penguins (Vanstreels et al. 2011), with some being more invasive than others. Techniques such as laparotomy (Risser 1971) and laparoscopy (Richner 1989) enable the determination of sex of live birds through visual examination of the gonads, but they are invasive, expensive, time consuming and require specialist skills as they can cause injury to the bird (Griffiths et al. 1998). Molecular techniques use PCR amplification of DNA to determine sex (e.g. Griffiths et al. 1998), enabling accurate and less invasive sex determination. These typically require blood samples as blood is a rich source of nuclear DNA. Molecular sexing birds from plucked feather samples is also possible and considered to be less invasive (Harvey et al. 2006, Costantini et al. 2008). Other alternatives such as cloacal examination (Sladen 1978) can be done in the field but require additional handling time and the insertion of a cloacascope instrument. Determining sex by vent measurements was investigated in Magellanic Penguins (*Spheniscus magellanicus*) (Boersma and Davies 1987) but reliable estimates using this method were only possible for breeding birds and require knowledge of the egg-laying date relative to the date of measurement. Pichegru et al. (2013) successfully used this technique to sex incubating African Penguins. However individuals may abandon their nest in response to human presence, especially in the first days of incubation (Kemper 2007, Sherley et al. 2012) and disturbance during incubation can lead to egg losses to avian predators (Hockey and Hallinan 1981). Considering the African Penguin is listed as an 'Endangered' species (BirdLife International 2013), non-invasive techniques are the most appropriate.

In many sexually monomorphic bird species, slight dimorphic traits occur between male and female individuals (Ellrich et al. 2010). Discriminant function analysis of morphological measurements has been used to sex many penguin species, e.g. Chinstrap Penguins (*Pygoscelis Antarctica*) (Amat et al. 1993, Renner and Davis 1999, Polito et al. 2012), Magellanic Penguins *S. magellanicus* (Bertellotti et al. 2002, Vanstreels et al. 2011), Humboldt Penguins (*Spheniscus humboldti*) (Wallace et al. 2008), Little Penguin (*Eudyptula minor*)(Arnould et al. 2004), Northern Rockhopper (*Eudyptes moseleyi*) (Booth 2011) Southern Rockhopper Penguins (*Eudyptes* *chrysocome)* and Royal Penguins (*Eudyptes schlegeli*) (Hull 1996). The most frequently used morphological measurements are bill length and bill depth, but bill depth is generally the most important discriminating variable (Scolaro et al. 1983, Bertellotti et al. 2002, Wallace et al. 2008). Bill measurement is reliable because it does not fluctuate seasonally like body mass (Cooper 1972).

Cooper (1972) proposed sex determination for adult African Penguins based on bill length >58.5 mm for male and <57.0 mm for female, with comparison between partners for those birds that fall between these values (the male is assumed to be the bird with the greater bill depth). However, this does not enable sex determination of all individuals, especially if the partner is unknown or has not been measured. Pichegru et al. (2013) recently proposed a discriminant function method of sex determination using bill measurements for African Penguins. However, the bill depth method used is different from the historical measurement (Cooper 1972). No comparisons have been made to test whether these different measurement methods are equivalent.

This chapter examines African Penguin bill morphology. It clarifies whether the two bill depth measurement techniques in use are distinct. It then compares the discriminant sexing methods as described by Cooper (1972) and Pichegru et al. (2013) and that devised by Dani Farah. It explores the use of cutpoints with Farah's algorithm to increase classification accuracy. Lastly, it addresses bill morphometrics across colonies and regions, with birds sexed by molecular methods to clarify the appropriateness of applying these methods at different South African colonies.

Methods

Ethics

Field data were collected under Department of Environmental Affairs, SANParks and Cape Nature permits. All penguin handling was approved under the University of Cape Town Science Faculty Animal Ethics Committee or the Department of Environmental Affairs. Data were compiled from multiple research projects.

Data collection

Adult African Penguins are measured at rehabilitation centres, in captivity and in the wild for various research purposes. The bill measurements of adult African Penguins sexed in different ways were categorised into four groups: one of post-mortems, two wild bird groups and one of captive birds. Measurements were conducted at various locations (Table 2.1).

Table 2.1. Location and number of sexed adult African Penguin bill dimensions measured during post-mortems, in the wild and in captivity.

Study group	Measurement location	*N*
Post-mortem	SANCCOB, Table View, South Africa	*123*
Partner birds	Dassen Island, South Africa	*66*
	Robben Island, South Africa	*138*
DNA-sexed	Dassen Island, South Africa	*20*
	Robben Island, South Africa	*20*
	Boulders, South Africa	*20*
	Stony Point, South Africa	*20*
	Dyer Island, South Africa	*20*
	St.Croix Island, South Africa	*16*
	Bird Island, South Africa	*49*
	SANCCOB, Table View, South Africa	*57*
Captive	Adventure Aquarium, Camden, New Jersey, USA	*13*
	Caldwell Zoo, Tyler, Texas, USA	*9*
	Cheyenne Mountain Zoological Society, Colorado Springs, Colorado, USA	*17*
	Como Zoo, Saint Paul, Minnesota, USA	*3*
	Dallas Zoo, Dallas, Texas, USA	*10*
	Georgia Aquarium, Atlanta, Georgia, USA	*2*
	Henson Robinson Zoo, Springfield, Illinois, USA	*3*
	Jenkinson's Aquarium, Point Pleaseant Beach, New Jersey, USA	*10*
	Knoxville Zoological Gardens, Knoxville, Tennessee, USA	*6*
	Monterey Bay Aquarium, Monterey, California, USA	*11*
	Mystic Aquarium, Mystic, Connecticut, USA	*18*
	Newport Aquarium, Newport, Kentucky, USA	*4*
	Northeastern Wisconsin Zoo, Green Bay, Wisconsin, USA	*9*
	Omaha's Henry Doorly Zoo, Omaha, Nebraska, USA	*15*
	Racine Zoo, Racine, Wisconsin, USA	*1*
	Tautphaus Park Zoo, Idaho Falls, Idaho, USA	*17*
	Toledo Zoo, Toledo, Ohio, USA	*12*
	Tulsa Zoo, Tulsa, Oklahoma, USA	*12*
	Utah's Hogle Zoo, Salt Lake City, Utah, USA	*4*

Sick, oiled, injured and abandoned marine and coastal birds are frequently recovered and sent to the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) for examination and rehabilitation when possible (Parsons and Underhill 2005). SANCCOB conducts post-mortem examinations. Measurements and sexing were conducted during post-mortem examinations of 123 adult African Penguins between 2008 and 2012 at SANCCOB. This group is referred to hereafter as Post-mortem birds.

The wild adult African Penguin study groups were compiled from multiple investigations. A health survey took place from 2010 to 2012 during which blood samples and measurements were taken from adult African Penguins at South African colonies: Dassen Island (33°25'S, 18°05'E), Robben Island (33°47' S, 18°22'E), Boulders (34°11'S, 18°27'E), Stony Point (34°22'S, 18°53'E), Dyer Island (34°40'S, 19°25'E), St. Croix Island (33° 47'S, 25° 46'E) and Bird Island (35°50'S, 26°17'E). Also included in this group were 57 adult penguins admitted to SANCCOB from areas west of Cape Agulhas (Fig. 2.1). These birds are referred to as DNA-sexed birds hereafter because they were sexed using molecular methods (Table 2.1).

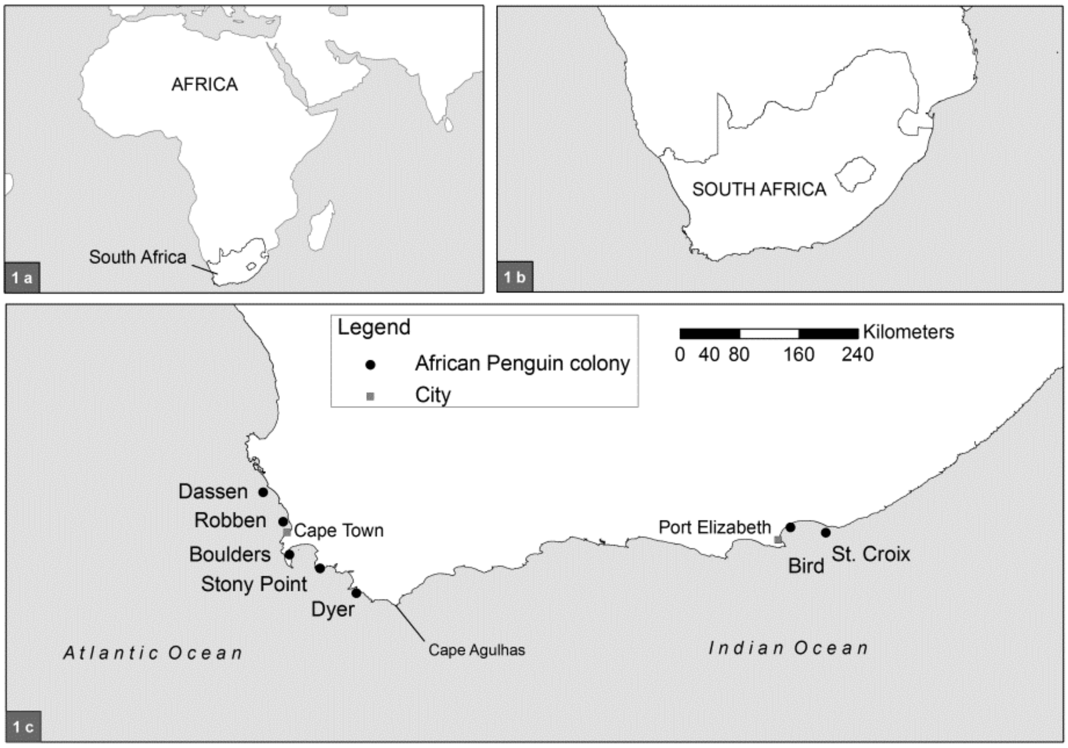

Figure 2.1. Map of the locations of the western and eastern African Penguin colonies sampled and their relative positions in South Africa.

The second wild bird group consisted of pairs of birds sampled at Robben Island and Dassen Island during foraging behaviour and survival research from 2008 to 2012 (Table 2.1). Birds raising chicks at a nest together are termed 'partners'. Measurements were taken of 117 breeding pairs, with sex determined by partner comparison. Pairs for which both bill length and depth were not larger for one of the birds of the pair were excluded (15 pairs) to avoid incorrect sex assignment in this discriminant function test group. This study group comprised 204 birds sexed by partner comparison, hereafter referred to as the 'Partner birds'.

Captive bird measurements were sourced from the African Penguin Species Survival Plan (SSP) program. The 176 Captive birds were measured at North American zoos and aquaria by various investigators from 2008 to 2009 (Table 2.1).

Bill measurements

We measured culmen or bill length (BL) and bill depth (BD_1) using Vernier callipers to 0.1 mm following Cooper (1972) (Fig. 2.2). Bill measurements of the Post-mortem birds and DNA-sexed birds were all taken by one investigator (NJP). Partner bird measurements were taken by multiple investigators. Within this study group, two measures of bill depth, BD_1 (measurement 1 on Fig. 2.2) and BD_2 (measurement 2 on Fig. 2.2, Pichegru et al. 2013) were made on 64 individuals at Robben Island in 2012 by KJR. The bill depth measurements on Captive birds were assumed to be BD_1 taken by multiple investigators.

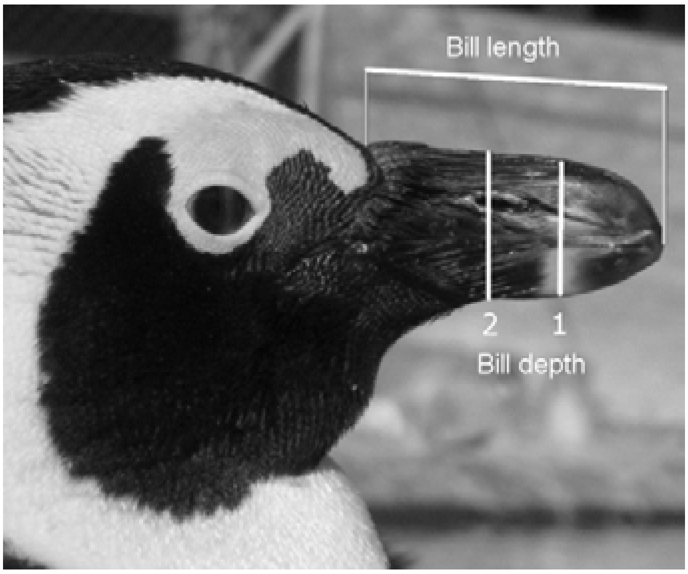

Figure 2.2. Bill measurements for the African Penguin:
Bill depth 1 BD_1 – taken from gonys (the ridge formed by the junction of the two halves of the lower mandible) located at the white stripe on the bill.
Bill depth 2 BD_2 – taken from point where feathers of throat meet the lower mandible.
Bill length BL – taken from the tip of the upper mandible to the base of the bill. The white line depicts the measurement while the light grey lines show where the callipers should be placed to take the measurement.

Sex determination

The sex of birds was determined differently for each study group. The Post-mortem group were sexed by visualization of the gonads (ovary or testes) and oviduct or *ductus deferens* (Hocken 2002). For the DNA-sexed birds, a drop of blood was collected on a strip of filter paper and placed in an Eppendorf tube, samples were stored at 5°C and sent to Molecular Diagnostic Services (MDS (Pty) Ltd.) for analysis. Avian genomic DNA was amplified by PCR using a target specific to the W chromosome, which is found only in female birds. Autosomal DNA material was amplified in both male and female birds, the PCR products were subjected to restriction enzyme digest followed by agarose gel electrophoresis and the resultant profiles were interpreted to obtain a male or female result. The birds in the Partner group were sexed by partner comparisons, as discussed above. Captive birds were sexed by a mixture of DNA sexing and observations of distinctive behaviours, such as egg-laying.

Analysis

A discriminant function analysis was conducted using *SPSS version 19* (IBM Corp 2010) with the Post-mortem bird bill measurements. To generate the discriminant function, sex of the bird was set as the grouping variable and the explanatory variables were bill length (BL) and bill depth (BD_1) with prior group probabilities computed from the actual group sizes. The discriminant function derived (composed of non-standardized coefficients) was used to generate scores for the original population and the accuracy of those scores was tested. Accuracy was determined for each sex as percentage classified correctly. The function's discriminant rate was investigated by using it to classify the birds from the original population and the DNA-sexed and Partner bird test groups. The accuracy of Farah's discriminant function that uses a classical Fisher's method for the discriminant function (hereafter the 'Farah discriminant function') was derived from the Post-mortem birds. We compared it with the Cooper (1972) methodology and the classical discriminant function presented by Pichegru et al. (2013) (hereafter the 'Pichegru discriminant function') where the appropriate bill depth measurements were available. Furthermore, we investigated using the range of discriminant function analysis scores of misclassifications in the original population as cutpoints to improve accuracy even more.

To examine whether the two techniques of measuring bill depth (BD_1 and BD_2) gave equivalent results, we used a paired *t*-test. We used a correlation and linear regression to investigate whether a conversion from BD_2 measurements to BD_1 was feasible. To assess differences in bill morphology between the captive and wild birds (Post-mortem, DNA-sexed and Partner combined), we compiled all bill measurements and examined normality of bill measurements using Shapiro-Wilk normality tests. We then tested for differences between means (Welch's *t*-test) and the distribution of measurements (Mann-Whitney-Wilcoxon test).

We tested colony and regional differences in bill length and bill depth BD_1 between the sexes using the DNA-sexed birds as they were all measured by the same investigator. We analysed sexes separately because samples sizes were unequal. We investigated differences in bill measurements between colonies with one way ANOVAs. The differences in bill measurements at a regional level between South African colonies west of Cape Agulhas and those east of Cape Agulhas (Fig. 2.1) were addressed with Welch's *t* test for unequal variances as sample sizes were not the same and thus likely to have dissimilar variances. Where appropriate, Tukey's post-hoc comparisons were used to identify significant differences.

Results

In the sample of 123 birds sexed via post-mortem used to derive the Farah discriminant function, males were found to have a culmen on average 8% larger and bill depth BD_1 10% larger than those of female African Penguins (Table 2.2). There was overlap in culmen and bill depth measurements between the sexes and both measurements showed approximately normal distributions for each sex (Fig. 2.3). The discriminant function is presented in Table 2.3 as well as other morphological methods for sex determination of adult African Penguins.

The Farah discriminant function correctly classified 92.7% of the individuals from which it was derived (Table 2.4). Within this sample, a total of nine individuals were incorrectly classified; six males out of 50 (12%) and three females out of 73 (4%) (Fig. 2.4). The mean Farah discriminant scores are listed in Table 2.2. The Farah discriminant function scores have less overlap between the sexes than the overlap between bill length and depth measurements (Fig. 2.3). No misclassifications occurred for scores >0.73 or <−0.93. There were 46 individuals (37% of total) between these margins with nine (20%) classified incorrectly indicating a 20% chance of error in prediction if the discriminant score fell between those two values. The Farah discriminant function correctly classified 89.6% of individuals sexed via molecular methods and 91.3% of individuals sexed from the measurements of the paired individuals (Table 2.4). The range of Farah scores for which wild birds were misclassified (Post-mortem, DNA-sexed and Partners groups combined) was −1.42 to 1.96. We found out of the total of 51 misclassifications 71% (36) were between the range of −0.5 and 0.5 and 90% (46) were between the range of −1 and 1. Of the wild bird scores, 93.5% (274) had scores of an absolute value greater than 1. Of these, five were misclassifications giving a 2% misclassification rate for scores greater than 1 or less than −1.

Table 2.2. Bill measurements and Farah discriminant function scores of 123 African Penguin sexed from post-mortem.

Parameter	Female (N = 73)		Male (N = 50)		Mean difference (95% Cl)	*t*-value	df	p-value
	Mean ± SD	Range	Mean ± SD	Range				
Bill length BL (mm)	55.1 ± 2.2	48.8 – 58.8	59.8 ± 2.1	55.5 – 65.0	4.7 (3.9 – 5.5)	11.95	108.22	<0.001
Bill depth BD_1 (mm)	21.8 ± 1.1	18.5 – 24.3	24.2 ± 1.4	21.2 – 28.5	2.4 (2.0 – 2.9)	10.43	93.56	<0.001
Discriminant function scores	-1.00 ± 1.00	-3.59 – 0.73	1.52 ± 1.10	-0.93 – 5.06				

Table 2.3. The functions and classification methods for sex determination of African Penguins developed and in the literature.

Function	Equation	Classification method	Data set	Type of sexing	Reference
Cooper[1]		BL > 58.5, then male BL < 57.0, then female	66 dead adults	Gonad visualization	Cooper 1972
Pichegru[2]	$C1=-350.677 + (7.589\ BL) + (9.320\ BD_2)$ $C2=-292.189 + (6.962\ BL) + (8.421\ BD_2)$	C1 > C2, then male C1 < C2, then female	218 live adults	Cloaca measurements (validated by 12 pairs sexed by DNA) and partner comparison	Pichegru et al. 2013
Farah[3]	$D=-27.698 + (0.304\ BL) + (0.456\ BD_1)$	D ≥ 0.5, then male D < 0.5, then female	123 dead adults	Gonad visualization	This paper
Farah with cutpoints		D > 0.726, then male D< −0.931, then female −0.931 ≥ D ≤ 0.726, then unclassified			This paper

[1] Bill length (BL) only

[2] Bill length (BL) and bill depth BD_2

[3] Bill length (BL) and bill depth BD_1

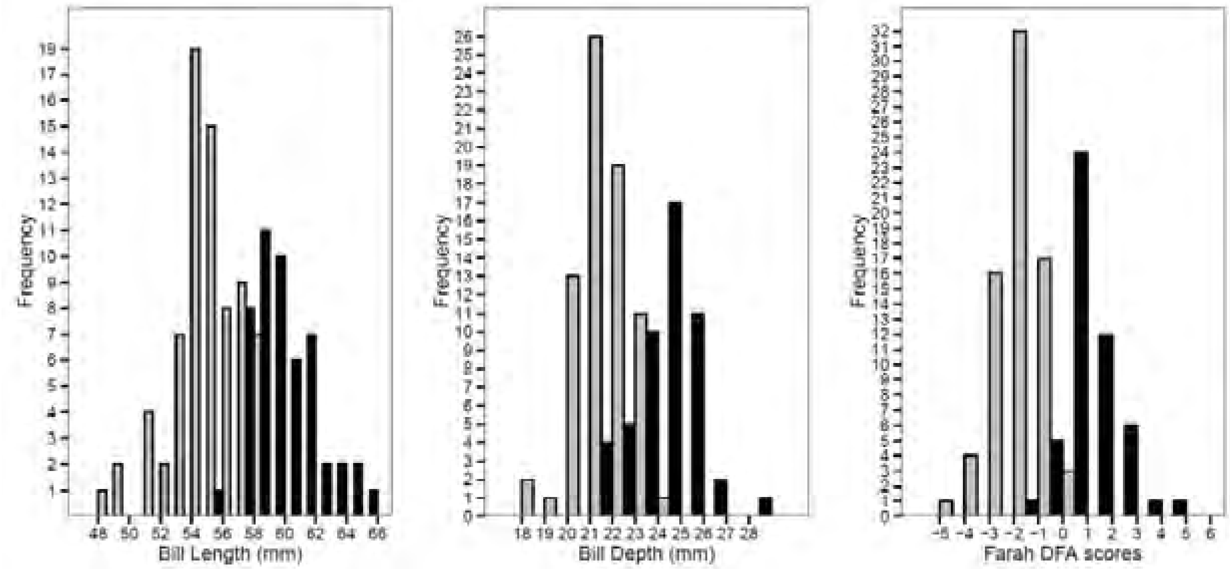

Figure 2.3. Frequency distributions for the bill length (mm), bill depth BD_1 (mm) and the Farah discriminant function analysis (DFA) scores showing bimodal distribution of the sexes with males (N = 50) shown in black and the females (N = 73) in grey for 123 African Penguins sexed by visualization of the gonads during post-mortem analysis.

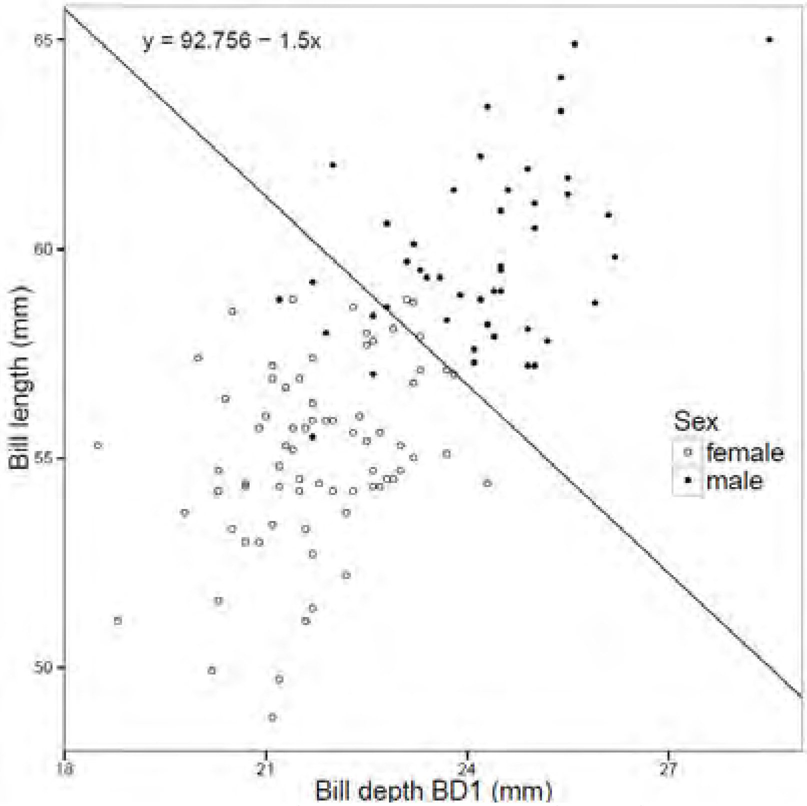

Figure 2.4. Scatter plot of bill measurements of 123 African Penguins sexed by post-mortem and used to devise the Farah discriminant function, males (N = 50) shown in solid black circles and the females (N = 73) in white circles. The line y = 92.756 - 1.500 x , where y is bill length in (mm) and x is bill depth BD_1 in (mm), shows the threshold for the Farah discriminant function. It classifies birds on and above this line as males and below as females.

The Farah discriminant function with cutpoints improved accuracy of the cross validation groups to 97% and 99% for the DNA-sexed and Partner birds, respectively. There was less of a difference in classification accuracy between the sexes (Table 2.4). However this increase in accuracy is at the expense of having some individuals remain unclassified, 16% and 29% of those respective test groups (Table 2.4).

When using bill depth BD_1 measurements, the Pichegru discriminant function correctly classified c. 80% of individuals in three test groups (Post-mortem, DNA-sexed, Partner) as this function was devised with the bill depth BD_2 measurement. While the two bill depth measurements were correlated ($r = 0.85$, $t_{59} = 12.2$, $p<0.001$), the paired *t*-test showed that the two bill depth measurements for 61 birds were not equivalent ($t_{60} = 10.6$, $p < 0.001$); the mean BD_2 value of 24.3 mm is 1.4 mm (95% CI: 1.14–1.68) greater than the mean BD_1 value of 22.9 mm. The linear model, $BD_2 = 3.055 + (0.928(BD_1))$ accounted for 71% of the variation in the data ($F_{1,59} = 148.8$, $p < 0.001$; adjusted R-squared = 0.711) but this regression does not explain a high enough proportion of the variation to adjust the Pichegru function for BD_1 measurements.

For the Partner birds where both bill depth BD_1 and BD_2 measurements were available, the Pichegru discriminant function correctly classified 90% using the BD_2 measurements of the individuals while the Farah discriminant function correctly assigned 92% using the BD_1 measurement (Table 2.4). Three of the 52 individuals (6%) were classified differently by the two methods.

The Cooper (1972) method did not provide a classification for all individuals; those with bill length measurements falling between 57.0 mm and 58.5 mm (78 samples from a total of 549, 14%) were unclassified (Table 2.4). Excluding the unclassified birds and calculating the classification accuracy as the percentage of the number of birds correctly sexed out of the number of birds classified is then 95%, 89% and 85%, respectively for the Post-mortem, Partner and DNA-Sexed birds. There was a bias towards predicting females because there was higher predictive success in classifying a female than a male bird in all classification methods, except in the accuracies of the Farah discriminant function with cutpoints, yet it leaves more females than males unclassified (Table 2.4).

Table 2.4. African Penguin sex classification accuracy comparisons of different discriminant methods.

Method used	Post-mortem birds Gonad visualization BD_1 measurement			DNA-sexed birds Molecular sexing BD_1 measurement			Partner birds Partner comparison BD_1 measurement			Partner birds Partner comparison BD_1 and BD_2 measurements		
Group	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Sample size	73	50	123	118	104	222	102	102	204	26	26	52
Cooper	78%[1]	74%[1]	76%[1]	89%[2]	60%[2]	76%[2]	88%[3]	66%[3]	76%[3]	92%[4]	81%[4]	87%[4]
Pichegru (uses BD_2)	nm	nm	nm	nm	nm	nm	nm	nm	nm	96%	85%	90%
Farah	96%	88%	93%	97%	81%	90%	99%	83%	91%	100%	85%	92%
Farah with cutpoints	100%[5]	100%[5]	100%[5]	97%[6]	96%[6]	97%[6]	98%[7]	99%[7]	99%[7]	100%[8]	100%[8]	100%[8]

1. In this case 25 birds (20%) were unclassified.
2. In this case 25 birds (11%) were unclassified.
3. In this case 29 birds (14%) were unclassified.
4. In this case 8 birds (1%) were unclassified.
5. In this case 46 (37%) birds were unclassified, 38 females and 8 males.
6. In this case 48 birds (16%) were unclassified, 28 females and 20 males.
7. In this case 60 birds (29%) were unclassified, 36 females and 24 males.
8. In this case 16 birds (31%) were unclassified, 11 females and 5 males.

nm - not measure

The mean bill length and depth measurements of captive birds were larger than those for wild birds and the distributions of the captive bird measurements differed from those of wild birds (Table 2.5). Therefore use of discriminant functions on captive birds will not give accurate sexing results; to confirm this we tested sexing of the Farah function and Cooper method on the Captive birds and found the accuracy rates to be 60 and 70%, respectively.

When we examined colony differences (Table 2.6), ANOVA revealed differences between colonies for female BD_1 measurements ($F_{6,79}$ = 2.73, p = 0.02) and for male BD_1 measurements ($F_{6,72}$ = 3.15, p = 0.01). The ANOVAs for bill length measurements showed no significant differences between colonies for females ($F_{6,79}$ = 1.23, p=0.30) and males ($F_{6,72}$ = 0.81, p = 0.57). The post-hoc tests revealed the significant female bill depth BD_1 average difference of 1.4 mm between St Croix Island and Stony Point (p = 0.050); while for male BD_1 the significant average differences were 1.6 mm between Dassen Island and Stony Point (p = 0.02) and 1.3 mm between Robben Island and Stony Point (p = 0.04).

Regionally, females differed in BD_1 by 0.6 mm ($t_{81.9}$ = 3.107, p = 0.003) (Table 2.6). Mean female BD_1 was larger at the western colonies than the eastern colonies (Table 2.6). As for male bill depth BD_1 was not significantly different between regions ($t_{71.6}$ = 1.206, p = 0.232). Males from western colonies had a mean BD_1 of 24.7 mm while those from eastern colonies were 24.5 mm. No significant differences were found regionally for bill length in either males or females (all p-values > 0.05).

Table 2.5. Bill dimensions measurements by multiple investigators of wild and captive African Penguins. Test statistics show differences between captive and wild bird mean measurements and distributions.

Group	**Females (mean ± SD)**			**Males (mean ± SD)**		
	Bill depth BD_1	**Bill length**	**N**	**Bill depth BD_1**	**Bill length**	**N**
Wild	21.82 ± 1.07	54.65 ± 2.11	293	24.31 ± 1.19	59.31 ± 2.35	256
(Shapiro-Wilk normality)	(*W* = 0.994, p = 0.35)	(*W* = 0.991, p = 0.07)		(*W* = 0.995, p = 0.63)	(*W* = 0.996, p = 0.68)	
Captive	26.08 ± 3.26	55.57 ± 4.62	82	29.23 ± 3.65	60.58 ± 4.38	94
(Shapiro-Wilk normality)	(*W* = 0.996, p = 0.003)	(*W* = 0.967, p = 0.03)		(*W* = 0.967, p = 0.02)	(*W* = 0.988, p = 0.58)	
Mean difference	4.26	0.92		4.92	1.27	
Welch's t-test	$t_{85.9}$ = 11.7, P<0.001	$t_{90.7}$ = 1.74, p=0.084		$t_{100.3}$ = 12.8, p<0.001	$t_{113.2}$ = 2.7, p=0.008	
Mann-Whitney-Wilcoxon	*W* = 2952.5, p<0.001	*W* = 10160, p = 0.033		*W* =3 184, p<0.001	*W* = 9758.5, p = 0.007	

Table 2.6. Bill depth (mm) and length (mm) measurements for sexed African penguins. The first three lines provide historical information presented by Cooper (1987) (birds sexed by gonad visualization), Duffy (1987) (partner comparison) and Pichegru et al. (2013) (cloaca measurements, DNA sexing and partner comparisons). The remaining rows contain the results of our DNA-sexed African Penguins measured by a single investigator (NJP) at series of colonies in western and eastern South Africa. The majority of bill depth measurements are BD1 taken at the stripe except for those in bold italics which are BD2 measurements taken at the base of the bill. The BD2 measurements presented for Robben Island were from birds sexed by partner comparison and measured by another investigator.

Category		Females (mean ± sd)			Males (mean ± sd)		
	Colonies	Bill depth	Bill length	N	Bill depth	Bill length	N
Cooper 1987	Dassen	21.0	55.5	25	23.0	60.5	41
Duffy 1987	Namibian colonies, Dassen and Dyer	22.3 ± 1.3	54.7 ± 2.2	127	24.8 ± 1.3	59.5 ± 2.4	127
Pichegru et al. 2013	Bird and St. Croix (Eastern colonies)	***23.1 ± 1.4***	55.5 ± 2.4	167	***25.9 ± 1.4***	60.3 ± 2.7	166
Colony	Dassen (Western)	22.4 ± 0.9	54.3 ± 1.8	14	23.7 ± 0.8	57.7 ± 3.4	6
	Robben (Western)	22.0 ± 0.9	54.0 ± 0.9	11	24.0 ± 0.9	58.7 ± 2.6	9
		22.7 ± 1.0		26	***25.8 ± 1.4***		26
	Boulders (Western)	22.7 ± 0.7	55.7 ± 1.3	6	24.7 ± 0.9	59.2 ± 2.6	14
	Stony Point (Western)	22.9 ± 0.9	53.8 ± 2.1	6	25.3 ± 1.2	59.6 ± 1.7	14
	Dyer (Western)	22.6 ± 1.1	54.6 ± 1.9	10	25.0 ± 1.3	58.5 ± 2.0	10
	St Croix (Eastern)	21.6 ± 1.0	55.0 ± 1.5	11	24.7 ± 0.6	57.9 ± 2.1	5
	Bird (Eastern)	22.0 ± 0.8	55.0 ± 1.7	28	24.4 ± 0.8	59.0 ± 2.0	21
Region	Western colonies	22.5 ± 0.9	54.4 ± 1.7	47	24.7 ± 1.2	58.9 ± 2.37	53
	Eastern colonies	21.8 ± 0.9	55.0 ± 1.7	39	24.5 ± 0.8	58.8 ± 2.0	26
Overall	All DNA-sexed birds	22.2 ± 1.0	54.7 ± 1.7	86	24.6 ± 1.1	58.9 ± 2.3	79

Discussion

The differences in the measurements of bill length and depth between adult male and female African Penguins allow for the possibility of determining the sex of individuals quickly and without invasive or molecular techniques through discriminant function analysis of bill measurements. As both bill measurements were found to be discriminating variables, care is required with the technique of bill depth and length measurements. The paired bill depth measurements (BD_1 and BD_2) were shown to be different measurements with an average difference of 1.4 mm. While this may seem small in magnitude (c. 5 – 8 % of bill depth measurements), nevertheless the discriminant functions rely on bill depth as a discriminating variable. Using a different depth measurement from the one with which the discriminant function is derived weakens the accuracy of sex determination. These two depth measurements should not be used interchangeably. A linear regression was insufficient to create a conversion between the two measurements without introducing a substantial amount of unexplained variation.

The Farah discriminant function was developed using individuals with sex confirmed from visualization of the gonads and cross-validated using all the test groups. The Farah discriminant function is simpler than the Pichegru discriminant function as it follows a Fisher method instead of a Mahalanobis approach (Green 1978). The Partner birds for which both bill depth measurements were collected allowed for a comparison of the Farah discriminant function and the Pichegru discriminant function, even though the sample size was small. The Farah and Pichegru discriminant functions had similar predictive success of 92% and 90%, respectively. Such results are similar to those of Pichegru et al. (2013). This indicates that both functions can be used for field studies with the caveat that there is a risk of misclassifying small males as females and large females as males. This is a common problem with sex determination based on discriminant functions (Vanstreels et al. 2011). Assessing the score value can help to ascertain the probability of misclassifications. The larger the absolute value of the score the less likely misclassifications are to have occurred. Awareness of discriminant function scores, which may lead to classification error, may help to minimize misclassification in practice. Misclassifications in wild birds occurred with Farah discriminant function analysis scores between −1.4172 and 1.9572. The sex determination of wild individuals with scores in this range should be treated with caution. The use of cutpoints improved the classification accuracy of the Farah discriminant function but at the cost of some birds remaining unclassified. This approach should be used with caution depending on the question of research. Brennan et al. (1991)demonstrated that having smaller sample sizes of more accurately classified birds lowered accuracy in determining sex ratios. Bill overgrowth is known to occur in captive penguins (Fiennes 1967, Wallace et al. 2008, pers. obs.). So the finding that the bill lengths and depths of captive African Penguins are greater than those of wild ones is as expected (Table 2.5). Therefore, these discriminant functions are only applicable to wild African Penguins, as in the sex determination of Humboldt Penguins (Wallace et al. 2008).

The culmen measurements obtained in this study were similar to those of Pichegru et al. (2013), Duffy (1987) and Cooper (1972) (Table 2.6). We did not find the trend noted in Duffy (1987) of the colonies furthest east and west having larger culmens. Duffy (1987) investigated colonies in Namibia and two along the west coast of South Africa, while our investigation was restricted to colonies along the coasts of South Africa. Furthermore, there was no significant differences in bill length between colonies or region.

In terms of bill depth BD_1, sample sizes were too small for conclusive results for colony comparisons. Where significant differences were found they were all less than 1.7 mm. The significant differences may well be artefacts due to small sample sizes. Pooling investigator data did not improve the sample sizes of all colonies and so did not provide more conclusive results. The significant regional difference found in females between western and eastern colonies of an average difference of 0.6 mm is small in magnitude (corresponding to 3% of total bill depth measurements) and probably not biologically meaningful especially as sample sizes are relatively small (Nakagawa and Cuthill 2007).

We found little evidence for bill morphology differences across geographical area (Table 2.6). This is as one would expect considering juveniles have been shown to cover substantial distances after fledging (Sherley et al. 2013) and to disperse to breed at colonies outside of their natal region in small numbers (Randall et al. 1987, Whittington et al. 2005); thus potentially mixing the genetic structure of colonies within each region.

Considering the similar predictive success of the different functions using bill length and depth measurements and that little difference in morphology was found between region and colonies, these discriminant functions have potential for wide use within the species' range. Therefore we conclude, as did Pichegru et al. (2013), that these methods should be applicable throughout South African penguin colonies. Further investigation however is needed before applying the sex discriminant functions to African Penguins in Namibia.

Ideally, measurements to assess regional differences in bill morphology should be made by the same investigator, but this is logistically difficult as the three breeding regions of African

Penguins are each separated by ca. 700 km. Hull (1996) reported differences in measurements taken between researchers studying Royal Penguins and cautioned against comparing studies conducted by different researchers. Hart et al. (2009) found observer error in Macaroni Penguin (*Eudyptes chrysolophus*) bill length and depth measurements to not be significant but also observed that inexperienced measurers deviated in their measurements more than experienced investigators did. For these reasons caution is needed before generalizing to all observers and especially in the case of long-term monitoring (Hart et al. 2009). Prior investigations into investigator differences in paired African Penguin measurements did not find significant differences between three investigators (Duffy 1987). Further investigation into investigator differences could be conducted on samples at post-mortem examination but the differences are likely to be larger with live birds as they can be moving during measurements or differences in handling technique. We recommend particular care in bill measurement technique for accurate sexing with the discriminant functions presented.

Due to the growing importance of persistent conservation efforts to preserve the African Penguin, the ability to determine the sex of an individual bird in the wild, without the necessity of further observations or tests, will aid future studies in understanding the movements and population dynamics of this species.

Conclusions

The two bill depth measurements in use differ by 1.4 mm. Thus, it is necessary to use the bill depth technique with which a discriminant function was derived to accurately sex African Penguins. Both the Pichegru discriminant function and the Farah discriminant function have similar accuracies when using the appropriate bill depth measurement. Using a cut point approach further increases accuracy. No geographical differences in bill morphology were found indicating the techniques presented can be used to sex birds throughout the species' South African range. The Farah discriminant function provides a sexing method which can be used to investigate for sex-specific differences in foraging behaviour.

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Chapter 3

A body condition index for adult African Penguins

Body condition indices from morphological measurements are used as indicators of body fat or energy reserves and are worth consideration in avian reproduction and behavioural studies. Adult African Penguins (*Spheniscus demersus*) vary in structural size making mass alone a poor indicator of condition. An adult body condition index for African Penguins would be useful for field research and conservation efforts. Condition indices are typically developed with multiple size measurements. However, due to the species' 'Endangered' status, minimal handling of birds is required in the field. This chapter develops a body condition index (BCI) following a quantile regression approach for adult penguins using a minimum of morphological measurements from a total of 1,453 adult measurements taken throughout the African Penguin's range (Namibian and South African coasts). This approach has two advantages over using the residuals of a regression for a BCI: (1) a quantile approach can account for heteroscedasticity in the data should it exist and (2) it is easier to understand conceptually than residuals. The body condition index provides another intrinsic factor with which to examine foraging behaviour. It could also be used for comparative field studies (temporal or spatial) and to improve release criteria at rehabilitation centres.

Introduction

Body condition indices are valuable in seabird ecology because they can provide information on the health of populations (Mallory et al. 2010). Morphological indices of body condition which adjust body mass for an individual's size can be better predictors of lipids than body mass alone for seabirds with high body lipid content (Jacobs et al. 2012). While there is controversy and considerable debate over which methods best reflect body condition there is general agreement that they need to be described in detail and empirically validated (Labocha and Hayes 2012).

Adequate metabolic reserves are physiologically important for survival and reproduction; this is especially the case for penguins. All penguin species fast during moult and some species fast for extended periods during breeding, the longest fasts being those by Emperor Penguins (*Aptenodytes forsteri*) of approximately 100 days (Croxall and Davis 1999). Larger penguin species can store proportionally more reserves than smaller species and fast and subsist on them for longer periods (Croxall and Davis 1999). Adequate metabolic reserves are also needed for thermoregulation (particularly when at sea because seawater has a greater thermal conductivity than that of air); penguins maintain their body temperatures by increasing their metabolic rates (Williams 1995). In African Penguins, high heat loss when at sea is prevented by their activity levels in combination with their insulating waterproof feathers, thick dermis, and subcutaneous fat (Wilson and Grémillet 1996).

In temperate penguins species, body condition has been found to be related to breeding success (Yorio and Boersma 1994), provisioning behaviour (Numata et al. 2000, Saraux et al. 2011), breeding timing and synchrony (Robinson et al. 2005) and having carry-over effects from the period prior to breeding (Salton et al. 2015, Tol 2015). In Magellanic Penguins (*Spheniscus magellanicus*), body condition was found to be the most important factor in explaining nest desertions (Yorio and Boersma 1994). Egg desertion and foraging trip duration was found to be related to body condition of Little Penguins (Numata et al. 2000). Furthermore, Little Penguin (*Eudyptula minor*) body mass at trip departure was linked to longer provisioning trips (Saraux et al. 2011). There has been evidence of body mass having carry-over effects on breeding success in Little Penguins (Salton et al. 2015)and African Penguins (Tol 2015).

An indicator of body condition in adult African Penguins has wide conservation and research applications. An adult body condition index would provide a method to compare adults at different colonies, localities, and seasons of the year; facilitating spatial and temporal comparisons within and between colonies. Such information might help to identify why some colonies have greater reproductive success and growth than others. It could also assist in the identification of how different parts of the life-cycle influence each other. Furthermore, and most relevant here, is that it would provide another intrinsic factor with which to examine foraging behaviour of adult African Penguins provisioning chicks.

Currently, the quantitative indicator of adult African Penguin body condition in use is body mass (Parsons and Underhill 2005, Pichegru et al. 2012). The penguin rehabilitation centre, the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB), use 2.8 kg as a release criteria (Parsons and Underhill 2005). This can also be thought of as a body mass threshold above which the centre is prepared to release penguins in rehabilitation. Adult penguin body mass has been used as a response variable to investigate purse-seine fishing closures (Pichegru et al. 2012). However, considering the range in adult African Penguins, body mass alone may not be representative of fat reserves for all individuals.

There are factors that influence body mass which need to be considered such as measurement time of day and life-cycle phase. This is because they could potentially skew body condition sampling if not accounted for. The mass of a breeding African Penguin can change over a day, with mass generally decreasing while on a nest and increasing when away foraging (Nagy et al. 1984). The mean daily change in body mass observed from ten African Penguins was a gain of 3% (range: 0 – 11%)when away from the nest and a decrease of 5% (range: 3 – 10%) (Nagy et al. 1984). Premoult adult penguins were found to be on average 968 g (31%) heavier than breeding adults and post-moult adults were on average 680 g (22%) lighter than breeding adults; carcass analysis indicated African Penguins lose on average 47% of their mass, 56% of their fat and 45% of their water during moult (Cooper 1978).

Another factor that needs to be considered for breeding adults provisioning chicks is the contribution of prey load to a body condition index. Penguins forage at sea and then return to their nests to regurgitate undigested prey load to their chicks. The undigested prey load which would be regurgitated would increase mass but the adult does not digest that prey themselves. To my knowledge, the maximum difference in body mass observed between African Penguins pre- and post-foraging is 0.8 kg (Wilson et al. 1989); this is also the maximum food mass obtained from 300 diet samples at Marcus Island (Wilson 1984). What is of interest is how much mass does a prey load add to body mass on average and how much the average prey load influences the body condition index?

An adult body condition index would allow for two useful applications. Firstly, as a tool to explore body condition of the penguins in the foraging study which were sampled over the breeding season. Decreases in body lipids through the breeding season have been observed in seabirds (Jacobs et al. 2012). Thus, I hypothesised body condition of African Penguins at the same stage of chick raising over the breeding season would decline. A body condition index would allow for an exploration of body condition between and within years at the Robben Island colony. Secondly, a body condition index would allow for an exploration of release criterion of 2.8 kg. Penguins can range in structural size. I hypothesise that the release criterion is an inappropriate body mass for all adult penguins and that a body condition index could provide a more effective tool by allowing one to identify whether a penguin is above or below an average mass for its structural size.

This chapter presents a body condition index for adult African Penguins using quantile techniques and following the general approach of Lubbe et al. (2014). Validation is conducted using post-mortem fat assessments. The contribution of prey load is considered and suggestions made for effective sampling. Examples of adult body condition index applications are presented and explored. The advantages of a quantile body condition index as opposed to other indices (e.g., scaled-mass index or residuals of body mass regressed on a measure of body size) are outlined.

Methods

Data collection

Measurements of adult penguins which died during translocation following the Treasure oil spill in 2000 were used to investigate the relationship between size variables of bill length (culmen), flipper length and tarsus length, all measured to 0.1 mm with callipers by one investigator, Bruce Dyer. Measurements of African Penguin adults were compiled from field surveys and research of live birds throughout the range in South Africa and Namibia from 2008 to 2014 (Table 3.1). Penguins were sexed by partner comparisons or molecular methods, see Chapter 2 for further details. Body mass was measured using a harness and hand held digital balance or spring balance to a precision of at least 0.01 kg (Kemper 2007). Bill length (culmen) (Fig. 2.2), and head length which is from the tip of the bill to the ridge on the back of the skull were taken with callipers to 0.1 mm by multiple investigators. Those measurements were used to investigate the range in body mass and structural size of adult African Penguins and then to calculate an adult BCI.

Table 3.1. The locations and years of the 1,376 adult African Penguins in South Africa and Namibia for which both mass and bill length measurements were available and used to develop the adult body condition index with bill length ($BCI_{\text{bill length}}$). Bill length was the variable used to indicate body size.

Colony	N	Year sampled
Mercury Island, Namibia	34	2008 2009 2010
Halifax Island, Namibia	45	2009 2010 2012
Dassen Island, South Africa (west coast)	298	2008 2009 2010 2011 2012 2013
Robben Island, South Africa (west coast)	406	2008 2009 2011 2012 2013, 2014
Boulders Beach, South Africa (west coast)	20	2012
Stony Point, South Africa (west coast)	64	2010 2013
Dyer Island, South Africa (west coast)	20	2010
St. Croix Island, South Africa (east coast)	181	2008 2009 2010 2011 2012 2013
Bird Island, South Africa (east coast)	308	2008 2009 2010 2011 2012 2013

Quantile body condition index approach

Applications of quantile regression can provide more complete pictures of ecological processes (Cade and Noon 2003). First presented by Koenker and Bassett (1978), quantile regression is an extension of linear regression modelling that enables the exploration of the relationship between a response variable and explanatory variable at different quantiles, or portions of the response variable (Koenker and Bassett 1978, Cade and Noon 2003, Koenker 2005). An advantage of quantile regression is that it can be applied when there is unequal variation between response and predictor variables (Cade and Noon 2003).Quantile regressions can be applied to the relationship between a species body mass and size (Lubbe et al. 2014).

The chick body condition index used measurements of chicks that were known to have fledged to create a comparative index (Lubbe et al. 2014). To adapt the method for adults requires a large sample size to account for adult body size and body mass variation. The 95% quantile regression was chosen to represent the upper predicted body mass of an adult penguin and the 5% quantile to represent the lower predicted body mass. Quantile regressions were performed for body mass as explained by a size variable, x. The quantile regression lines were used to calculate an adult body condition index (BCI) of an individual African Penguin:

$$\mathrm{BCI} = \frac{(\mathrm{M_i} - \mathrm{M_{5\%}})}{(\mathrm{M_{95\%}} - \mathrm{M_{5\%}})} \qquad \text{(eqn. 3.1)}$$

where M_i is the observed body mass of an individual penguin i of size variable x and $M_{5\%}$ and $M_{95\%}$ are the body mass at the 5% and 95% quantiles, respectively, at size variable x.

In this way, a penguin with a BCI of one is at the 95% quantile body mass for its size. An average body mass for a particular structural size would have a BCI of 0.5. Whereas a penguin at the 5% quantile body mass for its size would have a BCI of zero. This approach takes into account not only the body mass of the adult for its size but also the range of body masses that an adult can have for that size.

Different size variables to use with the BCI were explored. A different body condition method, the scaled-mass index by Peig and Green (2009) was conducted for comparison purposes. Only the quantile BCI using bill length ($\mathrm{BCI}_{\text{bill length}}$) is presented in detail as it gave the best results during validation.

Validation methodology

To investigate whether the body condition indices were representative of fat stores they were calculated for 133 adult African Penguins that died at SANCCOB from 2010 to 2014. During post-mortems, penguins were classified by veterinarians into four categories, based on the presence of fat and the prominence of the keel: 'Fat', 'Good', 'Moderate', 'Thin' or 'Emaciated'. A categorical regression using BCI as explained by the fat assessment categories was conducted to investigate whether variation in BCI gave significantly different mean values for those qualitative categories. The BCI was examined in relation to to bill size. An ANOVA was conducted to examine the BCI of penguins of different bill size quantiles.

The structural size of females is generally smaller than males (Chapter 2). However, if the relationship between the structural size measurements and body mass is the same proportionally for both sexes it should remove the necessity for a sex specific BCI. To address this, body mass as explained by bill length was examined for sexed birds. Following that, BCI of the sexes were compared. All statistics were conducted in R (R Core Team 2013).

Sampling considerations methodology

Prey load contribution to adult body condition index (BCI)

Diet samples were conducted on a monthly basis by the Department of Environmental Affairs (DEA) generally in late afternoon prior to sunset. Samples were taken by a water-offloading technique (Wilson 1984), with each bird flushed once (RJM Crawford pers. comm.). The average mass of a diet sample at Robben and Dassen Islands from 2011 to 2013 was calculated to estimate how much prey load may contribute to an adult's body mass upon its return to the colony. These are likely to be less than the actual prey load mass because penguins were flushed once and the entire stomach contents may not be obtained (Ludynia et al. 2010). I investigated how much the prey load mass might contribute theoretically to the BCI by adding those amounts to the actual body masses of all the birds and calculating the BCIs and examining the difference between the bird's actual BCI and the BCI of the body mass with the added prey load mass of interest. This was carried out for the median, mean, maximum diet sample mass and the observation of 0.8 kg by Wilson (1984).

Impacts of sampling timing to adult body condition index (BCI)

The time of day that measurements are collected may affect BCI. Breeding adult African Penguins are fairly synchronous in the foraging trip timing with most birds departing in the morning and returning in the evening (Wilson and Wilson 1990, Petersen et al. 2006, Ludynia 2007, Waller 2011). The departure and return times of breeding bird foraging trips were identified from the GPS-TDlog devices deployed on adult penguins provisioning for small chicks at Robben Island from May to August 2011, April to August in 2012 and May to June in 2013. The means (± SD) of departure and return times were calculated using circular statistics with the R package 'circular' (Agostinelli and Lund 2013).

Methods of application examples

Comparative field research

To provide an example of how BCI could be used to compare the variation in adult body condition at a colony over time, I explored the variation in BCI of African Penguins provisioning small chicks at the Robben Island colony. These adult measurements were collected during foraging research conducted from 2011 to 2013. Statistical differences in body condition were tested for with a linear model with month nested in year.

Release criteria

Release criteria are important guidelines for determining when birds are in optimum condition for release after receiving veterinary care at rehabilitation centres. It is important to minimise the time in captivity as it can involve various sources of stress reviewed by Morgan and Tromborg (2007), exposure to diseases and disruptions to natural life-history rhythms (Parsons and Underhill 2005). The adult BCI could be used to improve release criteria. To investigate whether the birds were in average (or above average) body mass for their body size, I calculated the BCI scores for a sample of penguins that had obtained the mass criteria (≥ 2.8 kg) and had been released from SANCCOB.

Results

The size variables of bill length, flipper length and tarsus length were measured for 194 adult African Penguins which had died during translocation in 2000. Bill length correlated with flipper length $r = 0.59$ (95% CI: 0.48–0.67, $t_{192} = 10.0$, $p < 0.001$) and moderately with tarsus length $r = 0.33$ (95% CI: 0.20–0.45, $t_{192} = 4.8$, $p < 0.001$). Measurements were available for 1,453 adults measured in the field. Bill length was the structural size variable collected in the field most often (98% of measurements). Bill and head length measurements (N = 350) were correlated $r = 0.84$ (95% CI: 0.80–0.87), $t_{348} = 28.4$, $p < 0.001$). Both bill length and body mass measurements were available for 1,376 live wild adult African Penguins (Table 3.1), and were used to develop the body condition index using bill length. Of those individuals, 851 were breeding at the time of measurement. The range in body mass was from 1.90 kg to 4.55 kg and the mean (± SD) was 2.92 ± 0.40 kg (95% CI: 2.90−2.94) (Fig. 3.1). The confidence intervals for the coefficients and slopes of the 95% and 5% quantile lines are provided in Table 3.2.

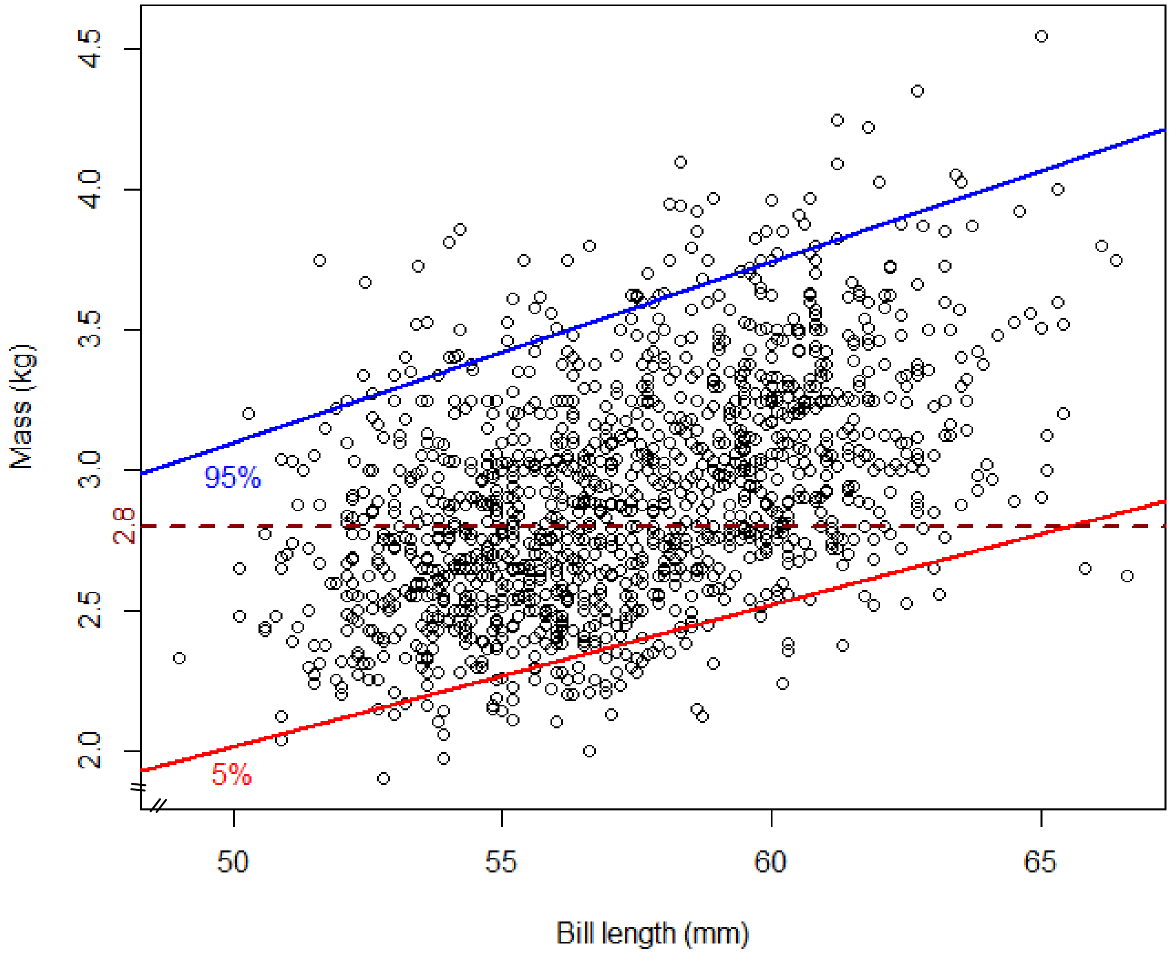

Figure 3.1. Scatter plot of body mass (kg) and bill length (mm) of adult African Penguins (N = 1,376). The 95% quantile regression line is shown in blue (y = 0.07x−0.14) and the 5% quantile regression (y = 0.05x−0.52) is shown in red. The quantile lines can be used to estimate a body condition index for an adult penguin of a particular bill length and mass. The dashed line is at 2.8 kg which has been used as release criterion for adult penguins at the SANCCOB rehabilitation centre (Parsons and Underhill 2005).

Table 3.2. Quantile regression lines of adult African Penguin (N = 1,376) mass (kg) as explained by bill length (mm) with 95% confidence intervals (CI).

Explanatory variable	Quantile τ values	Coefficient (95% CI) (kg/mm)	Intercept (95% CI) (kg)
Bill length (mm)	0.05	0.05 (0.04 – 0.06)	−0.52 (−1.22 – 0.33)
	0.95	0.07 (0.05 – 0.07)	−0.14 (−0.74 – 0.45)

The following equations are used to calculate body condition index using bill length as a size variable.

The body mass (kg) at the 5% quantile, $M_{5\%}$,is given by:

$M_{5\%} = 0.05x_i - 0.52$ (eqn. 3.2)
where x is the bill length size (mm) size of individual i

The body mass (kg) at the 95% quantile, $M_{95\%,}$ is given by:
$M_{95\%} = 0.07x_i - 0.14$ (eqn. 3.3)
where x is the bill length size (mm) size of the individual i

Substituting these values into Equation 3.1 gives the body condition index (BCI) using bill length as the size variable, $BCI_{\text{bill length}} = (M_i - M_{5\%})/(M_{95\%} - M_{5\%})$. This ratio is simply the difference between the actual body mass of the bird and the predicted body mass at the 5% quantile for that bill length size over the range of body masses from the 5% quantile to the 95% quantile, for that bill length size.

For comparison purposes, a scaled mass index was calculated following Peig and Green's (2009). procedure and equation. They recommend using a single variable for the size variable of the scaled mass index, identified as the one that has the strongest correlation to mass on the log-log scale. Head length had a higher correlation to mass (r = 0.61, 95% CI: 0.53–0.67) than bill length (r = 0.49, 95% CI: 0.41–0.57). The scaled mass index, which can be thought of as a predicted mass scaled to body size, was calculated for adult African Penguins using an individual's mass and the linear measure of head length standardized to average head length and scaled using the scaled mass index equation (Peig and Green 2009).

Validation of the body condition index (BCI) results

Measurements from adult birds that had qualitative fat assessments during post-mortems were used to assess the different body condition measures. The $BCI_{\text{bill length}}$ explained the fat categories ($F_{4,128} = 48.4$, adjusted $R^2 = 0.59$, $p < 0.001$) better than the predicted mass from the scaled-mass index ($F_{4,127} = 33.64$ adjusted $R^2 = 0.50$, $p<0.001$).

The mean BCI $_{\text{bill length}}$ values of birds in different fat categories were significantly different. Examining the post-hoc Tukey comparisons test showed BCI $_{\text{bill length}}$ values were all significantly different from each other in the different fat categories except for those in the Thin and Emaciated categories (Table 3.3).The BCI $_{\text{bill length}}$ scores of the birds in the categories of 'Fat, 'Good', 'Moderate', 'Thin' and 'Emaciated' showed distinct mean and median BCI scores for each of those categories (Table 3.3, Fig. 3.2).

Table 3.3. Tukey's Honest Significant Differences test results of the quantile body condition index using bill length as size variable (BCI $_{\text{bill length}}$) values of the different veterinary fat assessments of adult African Penguins, examined during post-mortems at SANCCOB. All categories were significantly different except for the thin and emaciated fat categories.

Condition comparison	Difference	Lower CI	Upper CI	p-value
Fat-Emaciated	1.446	1.093	1.798	<0.001
Good-Emaciated	0.936	0.699	1.172	<0.001
Moderate-Emaciated	0.573	0.317	0.830	<0.001
Thin-Emaciated	0.250	−0.083	0.583	0.24
Good-Fat	−0.510	−0.836	−0.184	<0.001
Moderate-Fat	−0.872	−1.213	−0.531	<0.001
Thin-Fat	−1.196	−1.597	−0.794	<0.001
Moderate-Good	−0.362	−0.582	−0.142	<0.001
Thin-Good	−0.686	−0.990	−0.381	<0.001
Thin-Moderate	−0.323	−0.644	−0.003	0.05

Table 3.4. Categorical regression results of the Body Condition Index using bill length (BCI $_{\text{bill length}}$) as explained by veterinary fat assessments categories for 133 adult African Penguins during post-mortems at SANCCOB rehabilitation centre.

Fat Assessment	Mean BCI estimate	Coefficient	SE	*t*	p-value
Emaciated	−0.388	−0.388	0.069	−5.59	<0.001
Thin	−0.138	0.250	0.120	2.08	0.04
Moderate	0.185	0.573	0.093	6.18	<0.001
Good	0.548	0.936	0.086	10.93	<0.001
Fat	1.052	1.446	0.127	11.35	<0.001

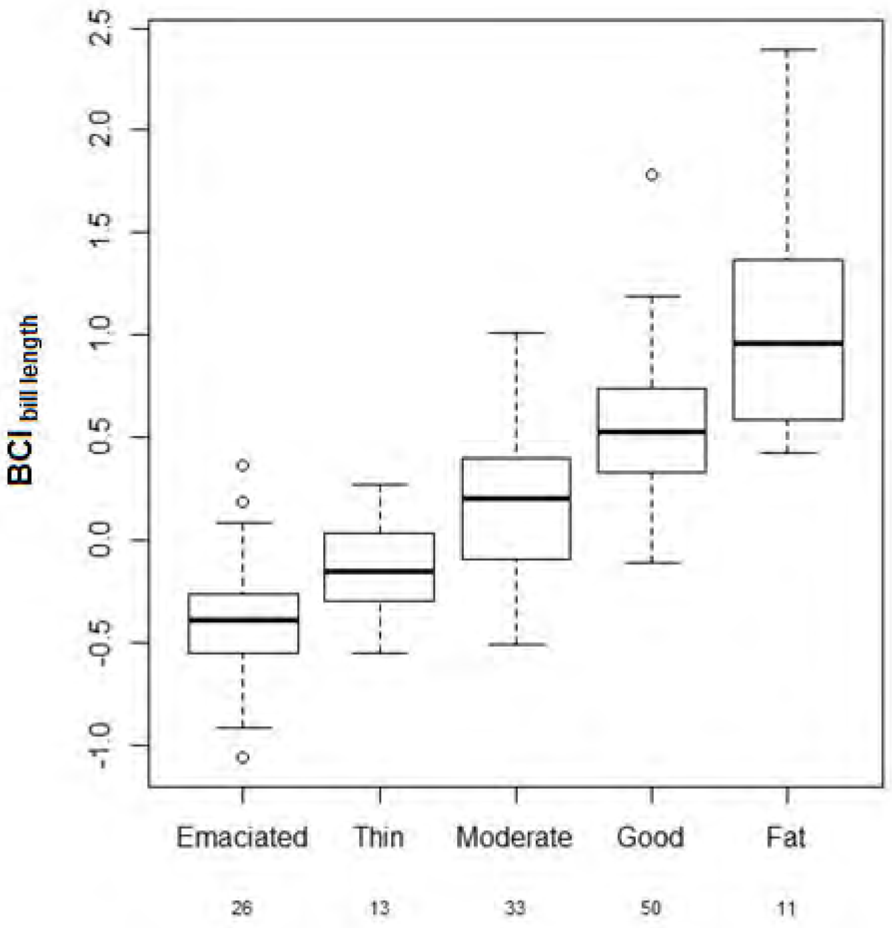

Figure 3.2. Box and whisker plots for body condition index using bill length (BCI $_{\text{bill length}}$) and body mass and from adult African Penguins that were assessed into qualitative fat categories during post-mortems (N = 133). The midline shows the median and the circles show the outlier values. The BCI medians are distinct for each qualitative fat category.

The mean ± SD BCI for the 1,376 adult African Penguins was 0.45 ± 0.30 (range: −0.30–1.50). The histogram of the BCI $_{\text{bill length}}$ values for all 1,376 birds was slightly skewed to the right (Fig. 3.3). The ANOVA comparing the mean BCI of the four groups of bill length sizes rejected the null hypothesis that the means were equal ($F_{3,\,1,372}$ = 5.35, p = 0.001). However, the categorical regression with quartiles as an explanatory variable showed that this model had an adjusted R^2 of 0.009, indicating that less than 1% of the variability in BCI was explained by quartile membership of bill size. Box plots of the BCI values in each group were similar indicating that the index is effectively accounting for the size of adult penguins (Fig. 3.4). Furthermore, plotting BCI $_{\text{bill length}}$ as explained by bill length showed no relationship between a bird's size and the body condition index (Fig. 3.5).

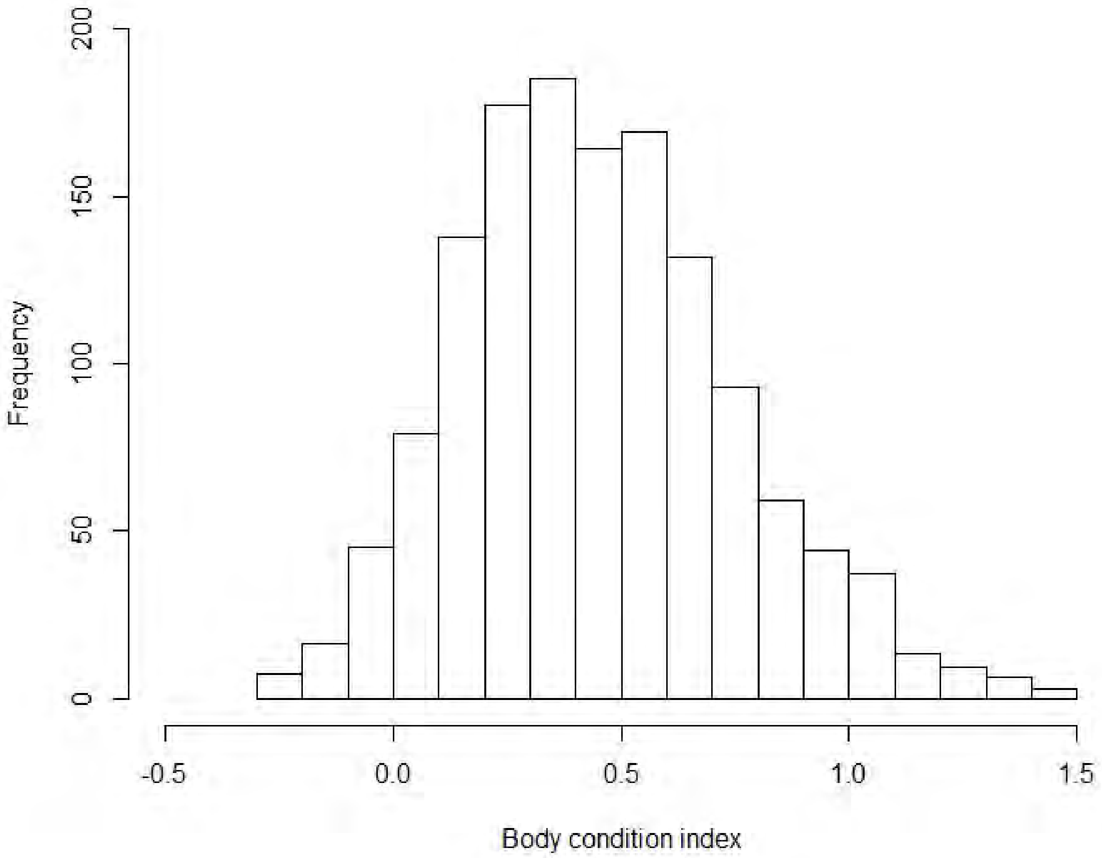

Figure 3.3. Histogram of the body condition of 1,376 adult African Penguins which were used to create the body condition index with bill length as a size variable and mass (BCI $_{\text{bill length}}$).

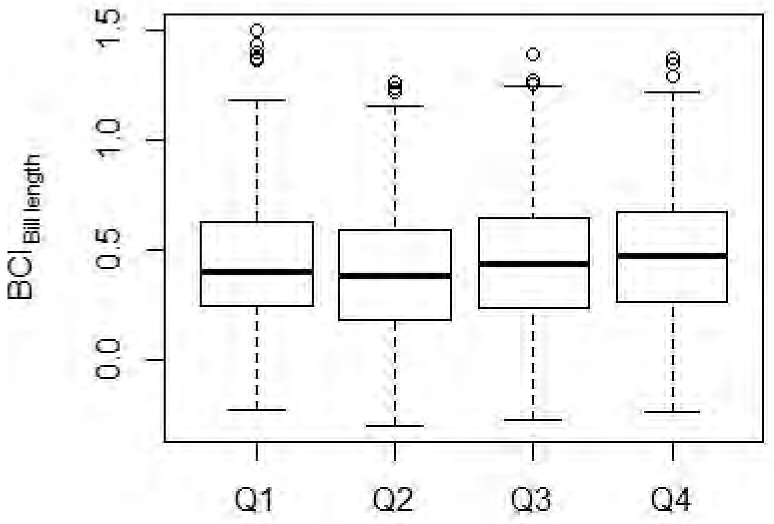

Figure 3.4. The Body Condition Index (BCI $_{\text{bill length}}$) which uses bill length as a size variable and mass for 1,376 African Penguin divided into quartiles of bill length, split at the 25th, 50th and 75th percentiles of bill length. The number of observations falling into each quartile is 344 and a box and whisker plot for each group of observations is shown. The midline is the median. The cut-points for the quartiles are at 54.9 mm, 57.2 mm and 59.8 mm. The box plots for each quantile show neither an increasing or decreasing pattern, demonstrating that BCI $_{\text{bill length}}$ effectively accounts for structural size .

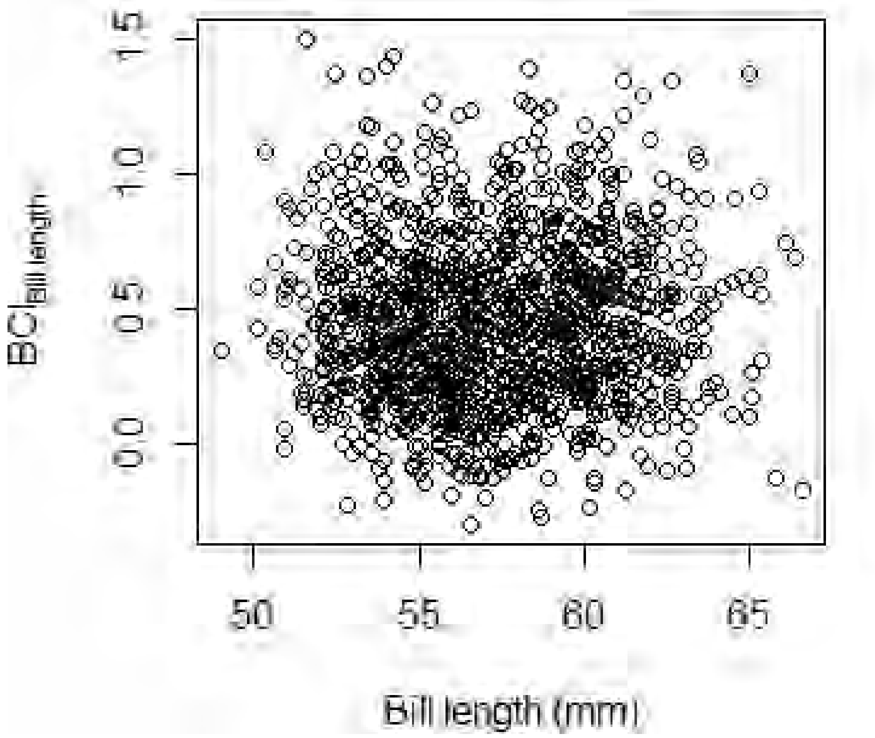

Figure 3.5. Scatter plot of bill length (mm) and Body Condition Index (BCI $_{\text{bill length}}$) calculated using bill length and mass of 1,376 adult African Penguins. The scatter plot shows that BCI$_{\text{bill length}}$ is not skewed for particular sizes.

African Penguins are sexually dimorphic in bill dimensions (Table 2.1, Fig. 2.3), head length and body mass (Fig. 3.6). The proportional relationship of body mass to bill or head length are similar for the sexes, both have slopes of 0.02 kg/mm (Fig 3.7). This indicates that sex-specific condition indices are unnecessary. There were measurements for 526 sexed adult African Penguins (266 females and 260 males) for which BCI could be calculated and compared. The sexes differed in BCI on average by 0.072 (95% CI: 0.022–0.123,t_{518} = 2.82, p = 0.005) females having a mean (± SD) BCI of 0.335 ± 0.313 and males having BCI of 0.408 ± 0.275 (Fig 3.8).

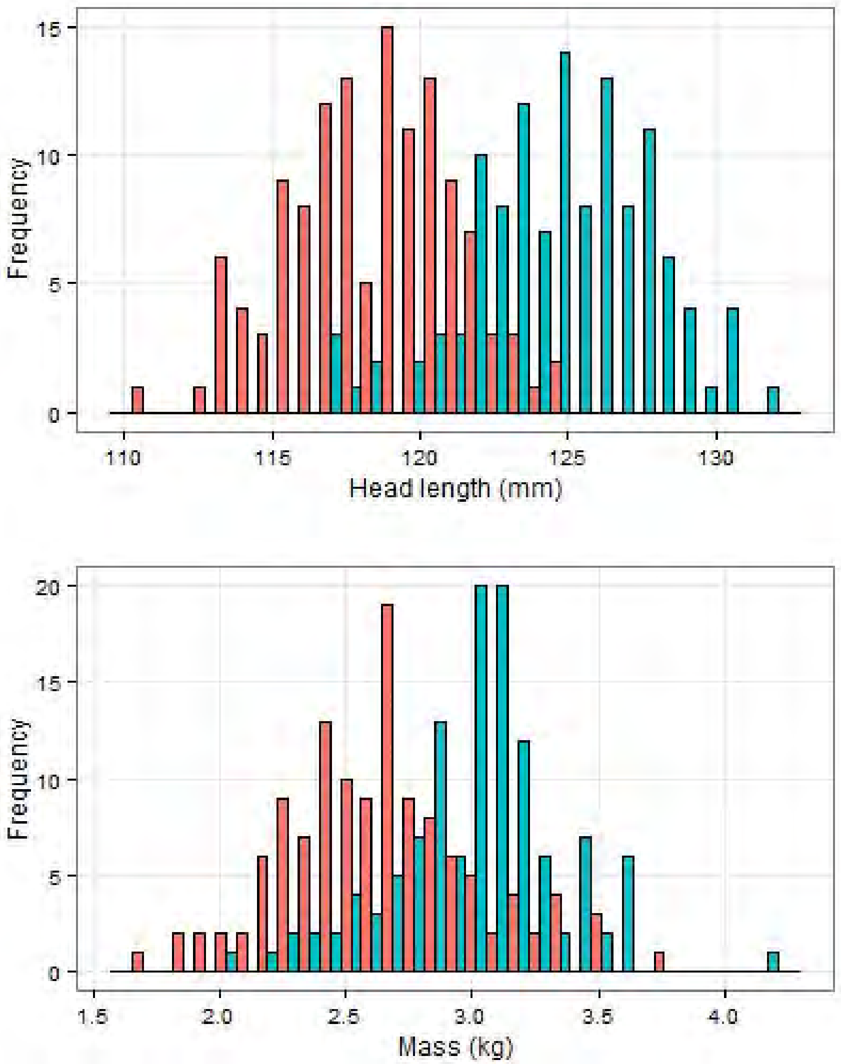

Figure 3.6. Histograms of the measurements of 248 DNA-sexed adult African Penguins (126 females in red, 122 males in blue). The birds are sexually dimorphic for head length (above) and for mass (below).

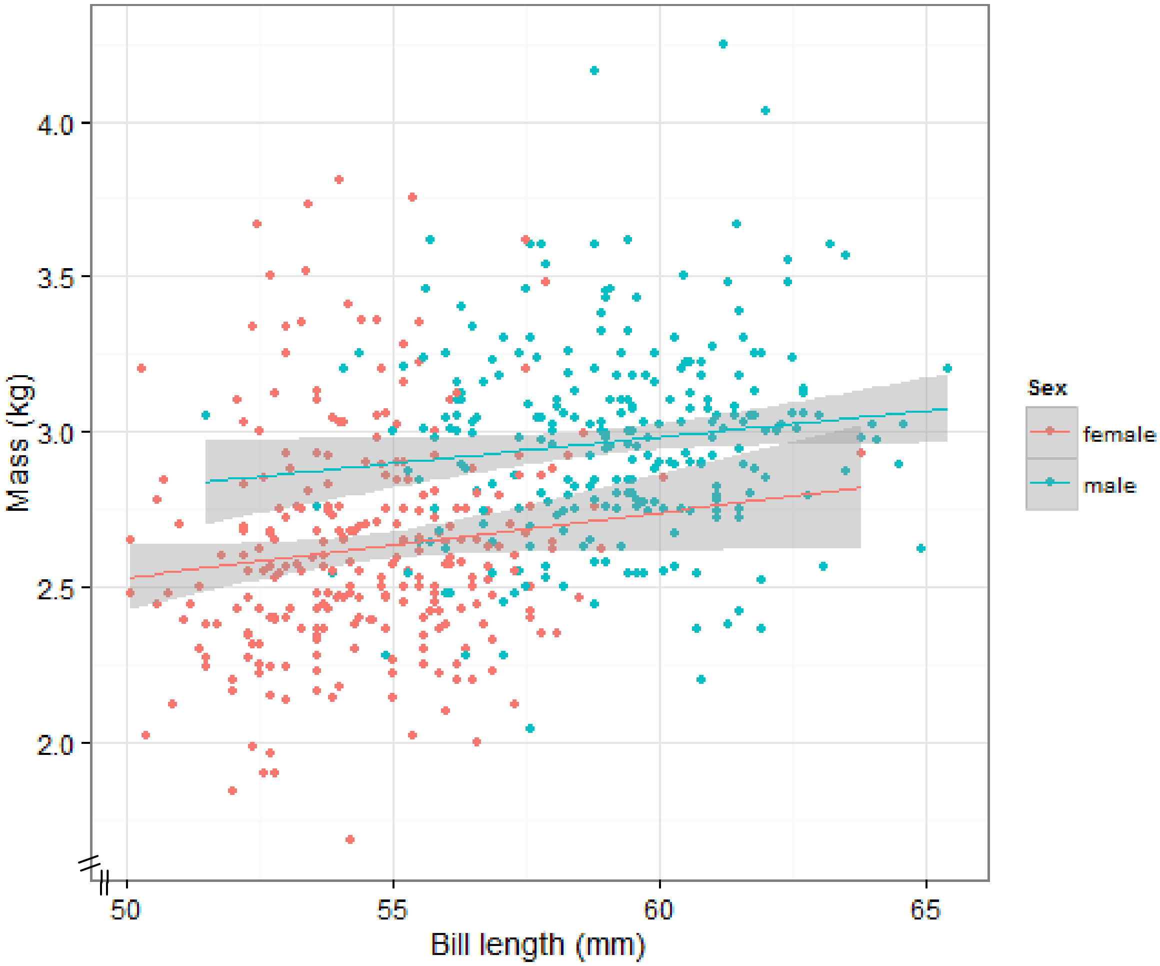

Figure3.7. Scatter plots with linear regression lines with 95% confidence intervals of mass as explained by bill length for adult African Penguins showing that the relationship is similar for both sexes in 526 sexed by various methods (266 females y = 0.02x + 1.48 and 260 males y = 0.02x ± 1.96). Females are shown in red and males in blue.

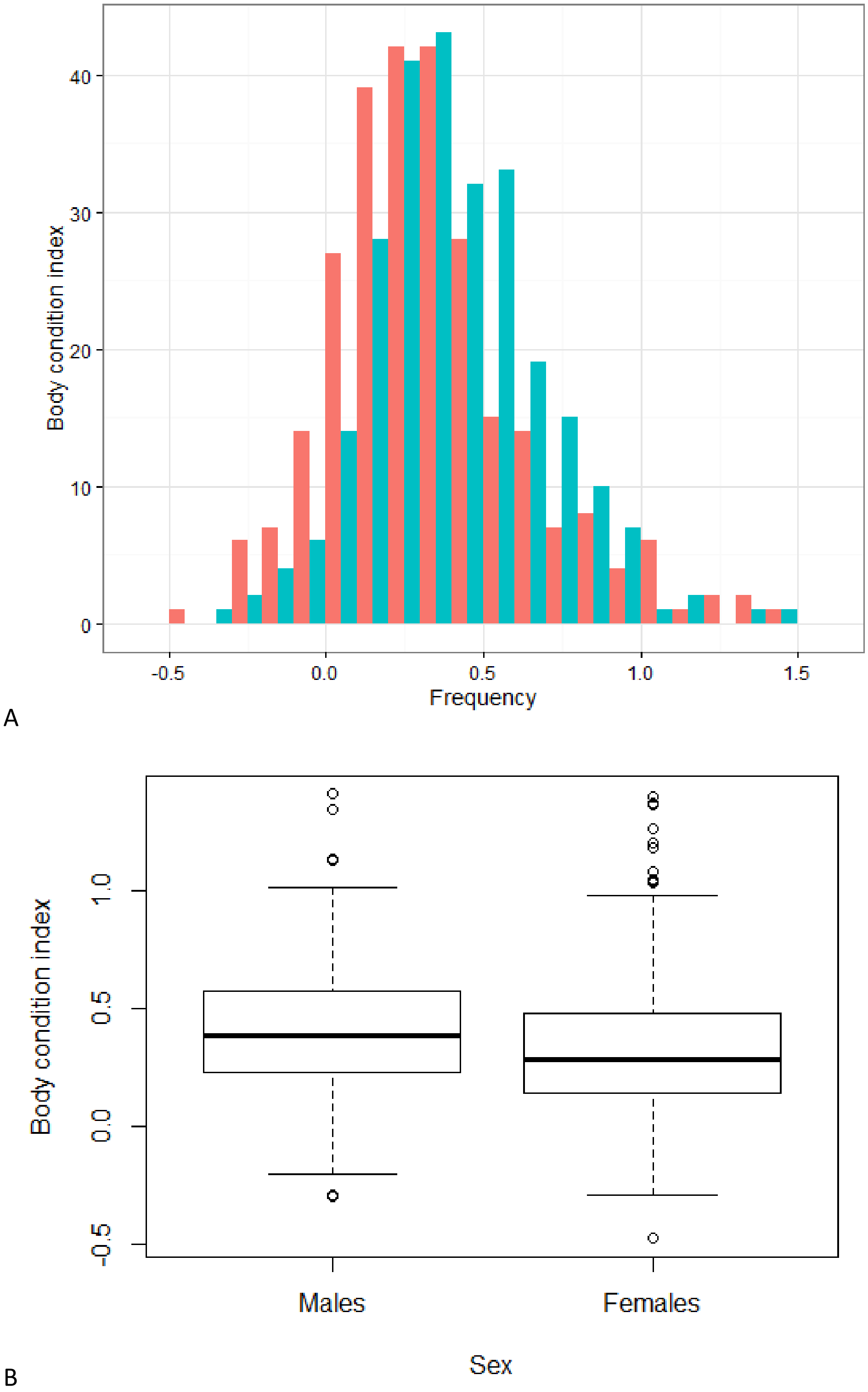

Figure 3.8. Body condition index using bill length and mass (BCI $_{\text{bill length}}$) calculated for 526 sexed African Penguins sampled in the field from South African colonies (278 sexed by partner comparisons and 248 DNA-sexed) for 266 females (red) and 260 males (blue) for which the (A) histogram of the sexes shows the distributions are similar with a unimodal peak and (B) box plots show the median BCI value for females (BCI $_{\text{bill length}}$ = 0.31) is lower than that of males (BCI $_{\text{bill length}}$= 0.39).

The mean BCI of birds known to be raising chicks was 0.449 ± 0.286 (N = 851) and 0.452 ± 0.314 for birds at an unknown life history stage (N = 525). A Welch *t*-test determined their average difference of 0.003 BCI (95% CI: −0.030–0.030) to not be significantly different ($t_{1029.9}$ = 0.17, p = 0.86). Plotting bill length to body mass showed breeders and birds of unknown life-history stage were distributed throughout the range of bird structural sizes (Fig. 3.9).

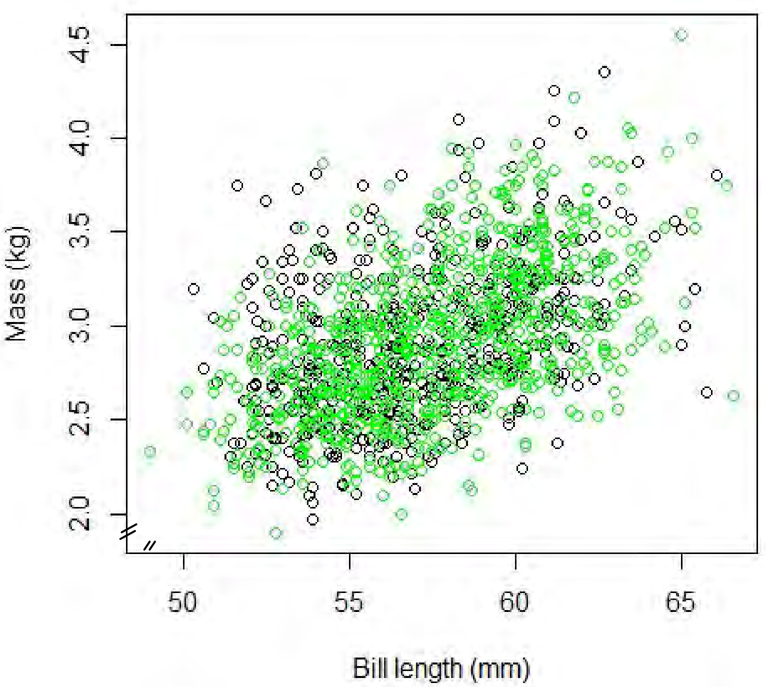

Figure 3.9. Scatter plot of bill length to mass for 1,376 adult African Penguins*;* black points are birds of unknown life history stage (N = 525) and the overlaid green points are adults known to be breeding (N = 851).

Results of sampling considerations

Prey load results

The diet sample masses collected at Robben and Dassen Islands were skewed to the right with 91% weighing less than 0.2 kg (Table 3.5, Fig. 3.10). The mean (± SE) diet sample prey mass was 0.0844 kg ± 0.004 kg (range: 0.0002–0.4691 kg) from 426 samples collected from 2008 to 2013. On Robben Island, the mean (± SE) diet sample mass from a total of 262 samples was 0.0919 kg± 0.0053 g (range: 0.0002–0.4400 kg). On Dassen, from a total of 164 samples over those years the average diet sample mass was 0.0725 kg ± 0.0059 kg (range: 0.0002–0.4691 kg). Considering the mean adult penguin mass of 2.9 kg (N = 1,376), a prey load of the maximum observed by Wilson (1984) of 0.8 kg, would mean a change of 28% of an average adult's body mass. However, the median (0.062 kg), average (0.084 kg) and maximum (0.469 kg) food masses calculated from the diet sampling at Robben and Dassen Islands would be 2%, 3%, and 16% of an average adult's body mass, respectively.

Table 3.5. African Penguin diet sample masses (g) collected at two Western Cape colonies Dassen and Robben Islands.

Colony	Year	Mean (g) ± SE	N	Minimum (g)	Maximum (g)
Dassen	2008	78.4 ± 9.7	60	0.2	294.0
Dassen	2009	60.0 ± 8.2	58	0.2	285.4
Dassen	2010	70.7 ± 12.4	28	0.2	303.6
Dassen	2011	56.8 ± 39.0	4	0.6	166.2
Dassen	2012	91.3 ± 45.1	3	3.3	152.1
Dassen	2013	110.2 ± 42.6	11	2.0	469.1
Robben	2008	82.2 ± 7.9	63	0.4	284.6
Robben	2009	106.8 ± 10.8	77	0.2	369.8
Robben	2010	86.0 ± 10.8	52	1.2	338.4
Robben	2011	89.5 ± 13.2	44	1.4	319.4
Robben	2012	176.9 ± 38.9	10	30.4	440.0
Robben	2013	31.4 ± 10.6	16	1.0	171.9

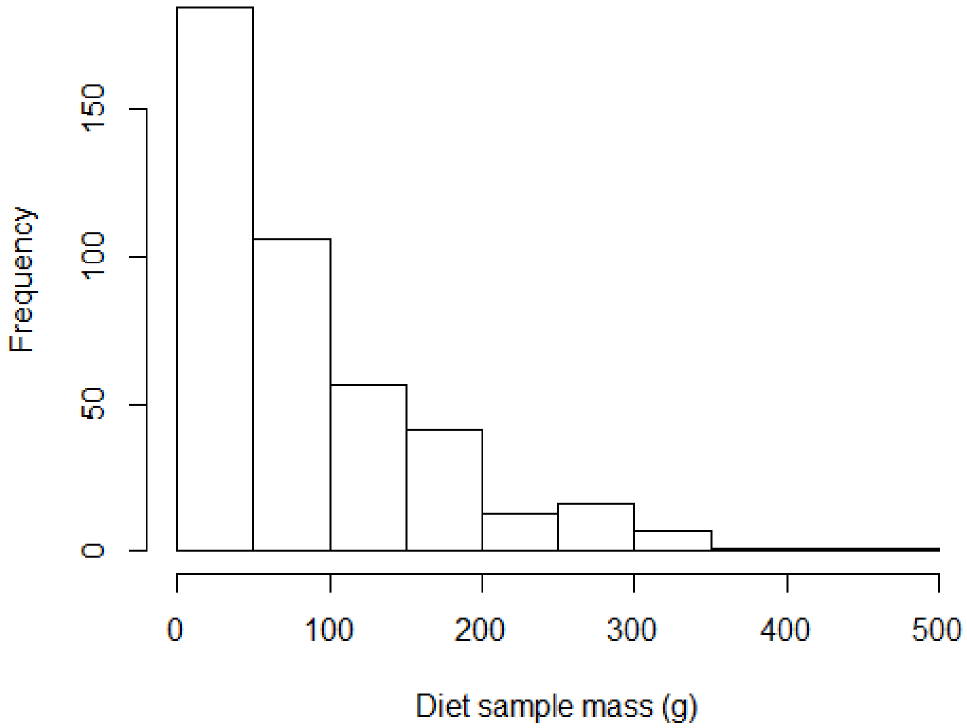

Figure 3.10. Histogram of the 426 diet samples collected from African Penguins at Robben and Dassen Islands from 2008 to 2013.

Estimates of the contributions of prey load to BCI results

To explore the potential influence of such prey loads to BCI $_{\text{bill length}}$, the median, average and maximum food mass samples observed at Robben and Dassen Islands and the maximum observed by Wilson (1989) were added to the actual body masses of all birds separately and BCIs were created for both the actual body masses and the theoretical body masses. The differences between those BCIs were largest for the smallest birds as one would expect. Adding the median and mean food mass samples to the body mass of all bird measurements created maximum BCI differences of 0.053 and 0.072, respectively (Table 3.6).

Table 3.6. The theoretical difference that the addition of different masses make to an adult African Penguin Body Condition Index using bill length (BCI $_{\text{bill length}}$) on the measurements of 1,376 individuals.

Source	Mass added (kg)	Mean BCI $_{\text{bill length}}$ difference (range)
Median diet sample mass observed	0.062	0.053 (0.048–0.057)
Mean diet sample mass observed	0.084	0.072 (0.064–0.077)
Maximum diet sample mass observed	0.469	0.397 (0.359–0.433)
Maximum change in mass between foraging trips (Wilson 1989)	0.800	0.678 (0.612–0.738)

Sampling time implications for methodology results

From the foraging data collected, the mean (± SD) time birds departed from Robben Island was 07:20 ± 00:18 (range: 03:55 to 14:43; N = 73) and the mean (± SD) return time was 17:35 ± 00:29 (range: 14:13 to 01:38; N = 74). There was a clear separation between departure and arrival times, with no birds returning to the island between dawn and 14:00 (Fig. 3.11).

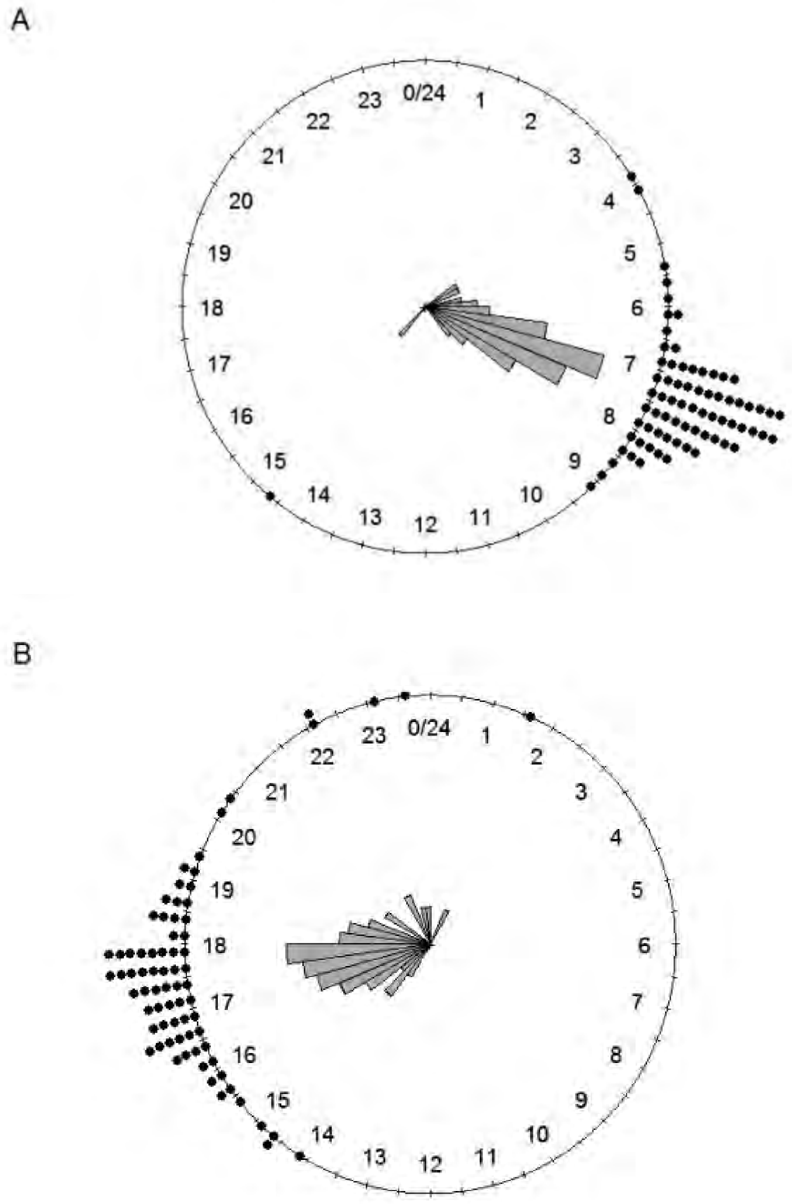

Figure 3.11. The timing of foraging trips of breeding African Penguins equipped with a GPS-TDlog device for one foraging trip from Robben Island from 2011 to 2013; (A) the departure from the island, when the bird entered the sea (N = 73) and (B) the return to the island, when the bird exited the sea (N = 74). In both circular plots, the time of day was split into 96 segments of a quarter of an hour. The rose diagram inside the plot split the data into 48 half hourly segments. Note the separation between departure and return times; departure is in the early morning and return is in the late afternoon and evening.

Results of application examples

Comparative field research application results

As an exploratory example, BCI $_{\text{bill length}}$ was calculated from the measurements of breeding adults collected from 2011 to 2013 at Robben Island for pairs of penguins raising small chicks in the foraging study (Fig. 3.12). Penguins were at the same life-history stage and efforts were made to measure both individuals of each pair giving approximately even sex ratios. In five cases, we failed to measure the partner. Sample sizes were small but there was no significant difference in mean BCI $_{\text{bill length}}$ between years (Fig. 3.12, A) or within years sampled (Fig. 3.12, B). Examining BCI $_{\text{bill length}}$ as explained by month nested in year also returned no significant results ($F_{10,142} = 1.49$, $p = 0.15$). The mean (± SE) body condition was 0.28 ± 0.02 BCI $_{\text{bill length}}$ indicating the penguins sampled were on average under the mean body mass for their body size.

Release criteria application results

Examining the data compiled to create the BCI showed that African Penguins with a body mass of ≥ 2.8 kg varied in bill length from 50.3 mm to 66.4 mm (Fig. 3.1).There were 27 birds measured in 2014 prior to release from SANCCOB that had obtained a body mass of 2.8 kg or more. The mean (± SD) body condition was 0.680 ± 0.04 (range: 0.079−1.097) BCI $_{\text{bill length}}$. Seven birds had a BCI $_{\text{bill length}}$ under 0.5 so were less than the average body mass for their structural size (Fig. 3.13). Their mean BCI value was 0.378 (range: 0.079−0.472). Those seven birds had bill lengths on average of 60.9 mm (range: 56.8−64.5 mm) and body mass on average 3.00 kg (range: 2.90−3.20 kg) indicating that although their body mass were greater than the release criterion, they were low for their large structural sizes.

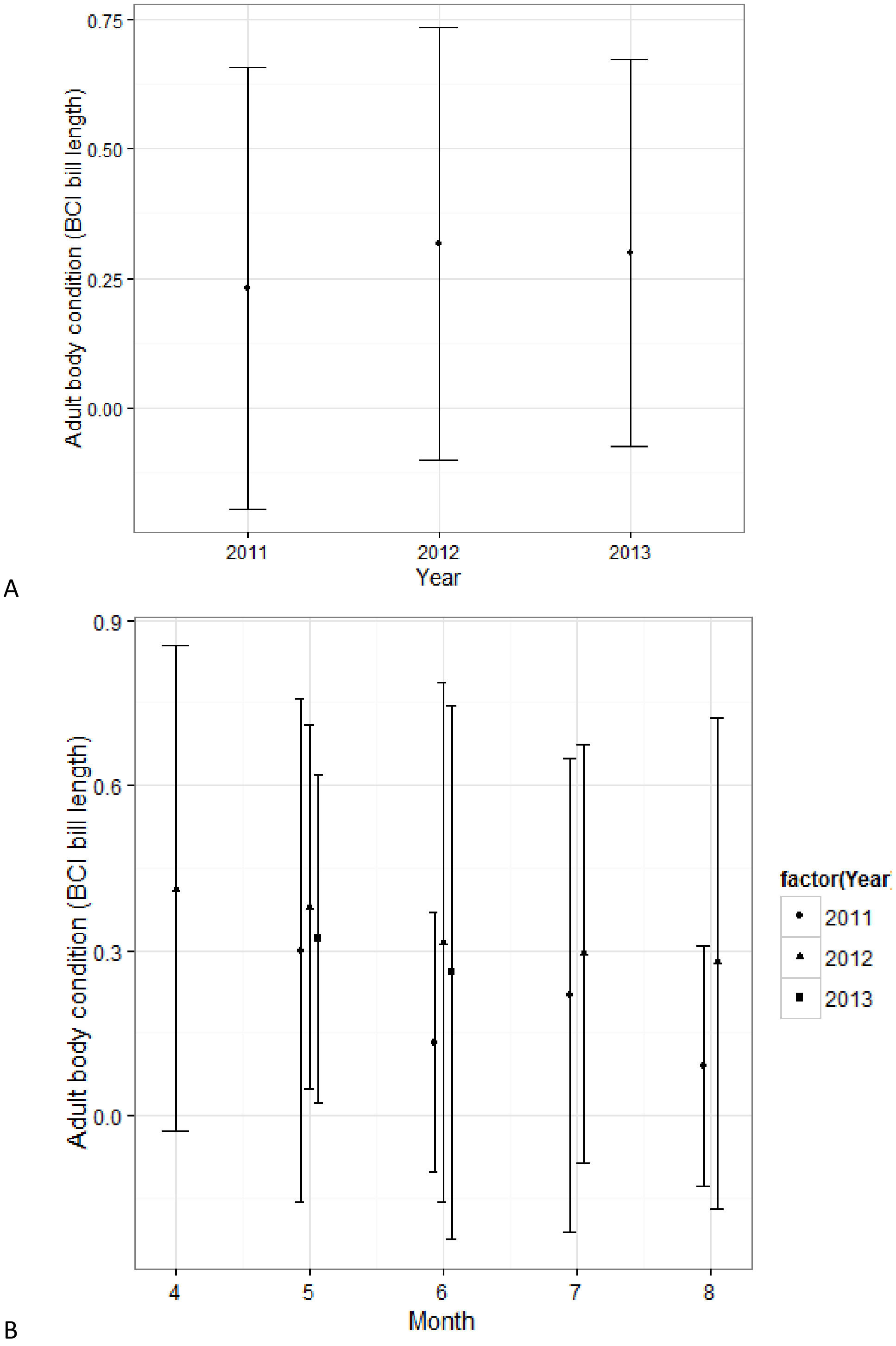

Figure 3.12 Mean Body Condition Index using bill length (BCI $_{\text{bill length}}$) with 95% confidence intervals for the African Penguins raising small chicks at Robben Island measured in the breeding season in 2011 [(N = 54) with 23 in May, 7 in June, 20 in July and 4 in August], 2012 [(N = 75) with 10 in April, 5 in May, 15 in June, 30 in July and 15 in August] and in 2013 [(N = 14) with 8 in May, 6 in June. Values were jittered so they do not overlap. There were no significant differences between years (A) or within years (B).

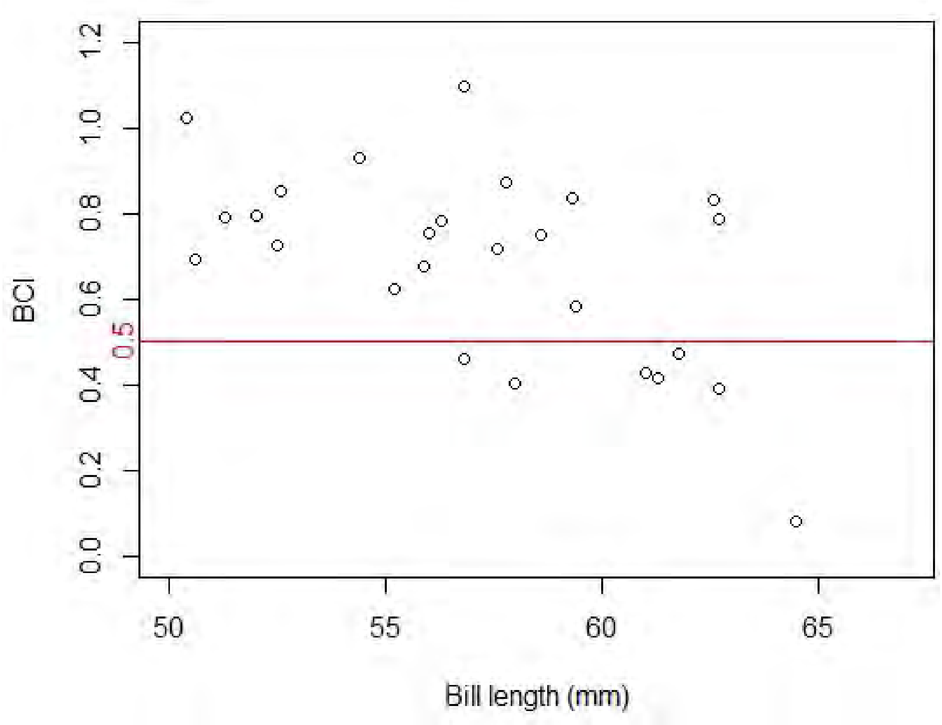

Figure 3.13. The body condition index (BCI $_{\text{bill length}}$) of the 27 adult African Penguins measured prior to release from SANCCOB rehabilitation centre. All had masses above 2.8 kg release criterion identified in (Parsons and Underhill 2005) but not all penguins had achieved a mass greater than the average for their size (the seven points below the red line). Note the bird with the lowest BCI also had the largest bill length.

Discussion

The quantile body condition index approach has advantages and takes a different approach from those reviewed in the literature (Jacobs et al. 2012, Labocha and Hayes 2012). The key advantage of this technique is that it permits heteroscedasticity of body mass in relation to structural size; that is, it does not assume that variability of body mass is the same for small birds and for large birds. This index does not correct body mass for size by a traditional ratio technique, ordinary least squares, or allometric method. It is a ratio that uses the difference of the bird's mass to the 5% quantile mass given that structural size and the range of body masses for African Penguin adults (between the 5% and 95% quantiles) given that structural size. It provides the ranges in body masses for structural sizes of African Penguins, from which further comparative studies can be made.

Body composition validation is recommended for body condition indices (Schamber et al. 2009, Jacobs et al. 2012, Labocha and Hayes 2012). Comparisons of the qualitative veterinary fat assessments indicate the $BCI_{\text{bill length}}$ presented is a useful quantitative tool to assess birds. The post-mortem assessment categories all had significantly different BCI values, except for the difference between the thin and emaciated categories, indicating the $BCI_{\text{bill length}}$ values reflect these qualitative fat scores (Table 3.3, Fig. 3.2). Model diagnostics showed that assumptions of categorical regression were valid. Nevertheless, investigations with larger category group sizes and further laboratory investigations are recommended.

It appears that even though the proportionality of bill size to body mass is similar for the sexes females often weigh less than males of the same size (Fig. 3.7). This could explain the slightly lower body condition found in females (Fig. 3.8). For breeding adults of the same size, it would be expected that females would be lighter than males because they would have lost body mass during egg-laying. Indeed, the data set is likely to comprise females that lost body mass during egg-laying so it seems reasonable to use a single $BCI_{\text{bill length}}$ for both sexes. Seabirds undergo changes in body composition during breeding and environmental stress (Jacobs et al. 2011). Interestingly, a study investigating in Magellanic Penguin (*Spheniscus magellanicus*) found females had higher total corticosterone levels than males but body conditions and mass were comparable between the sexes, indicating differences in stress physiology that could be connected to egg-laying (Villanueva et al. 2012). Further investigation in this in African Penguins is also worthwhile as it may help to explain the female-biased mortality being observed at SANCCOB (Pichegru and Parsons 2014).

The large sample of measurements (> 1,300) likely adequately captures the range in structural sizes of adult African Penguins (Fig. 3.1). Bill length is an easier measurement than flipper length or head length to take consistently on live penguins. It is important to note the condition index is only appropriate for wild penguins because bill overgrowth occurs in penguins in captivity for long periods (Fiennes 1967, Wallace et al. 2008), leading to bill dimensions which are different from those of wild penguins (Table 2.5). There is some heteroscedasticity in the data that can be seen in that there is a larger range in body masses for larger birds and the quantiles are not parallel (Fig. 3.1). This is further evidence that a quantile regression approach which allows for heteroscedasticity to be present in the data (Cade and Noon 2003) is more appropriate than the use of residuals. The histogram of $BCI_{\text{bill length}}$ values was skewed to the right which could be because penguins with extremely low body conditions are unlikely to survive and may be under represented or it could also be due to penguins with large prey loads or a combination of both.

Contributions of prey load to BCI $_{\text{bill length}}$

Diet samples identified that prey loads vary in mass (Table 3.5). On average the difference prey load makes to BCI $_{\text{bill length}}$ is small and biologically negligible; however, on the occasion that a bird has a particularly heavy prey load, it will increase the bird's body mass and BCI $_{\text{bill length}}$ substantially (Table 3.6). This has implications for comparative studies and it is worth keeping in mind that birds with heavy prey loads may skew the BCI $_{\text{bill length}}$ estimates. Therefore, careful sampling methodology is needed to avoid the bias associated with prey loads when carrying out comparative analysis. Specifically, measure body mass in the mornings prior to foraging.

Sampling implications to methodology

There is evidence that birds are synchronised in the departure and return of their foraging trips at Robben Island (Fig. 3.11). These timings coincide with previous findings at this colony and others (Wilson and Wilson 1990, Petersen et al. 2006, Ludynia 2007, Waller 2011). Departure times are strongly correlated with the time of sunrise, while the return times vary from late afternoon to evening (Wilson and Wilson 1990). Observations of penguins foraging in groups (Ryan et al. 2012) also indicate that there would be benefits to birds synchronising the timing of their foraging trips. If a bird is sampled in the evening it is likely to have a prey load because that is when chick begging and feeding takes place (Seddon and van Heezik 1993). Consequently, it seems likely heavy prey loads would be most likely to occur in the evening (Seddon and van Heezik 1993). For rigorous comparisons through time at a single colony or between breeding colonies conducting measurements in the mornings is recommended to reduce the potential bias from prey loads in breeding adults. Efforts should also be made to restrict sampling to particular life-history stages where possible.

Comparative field research

The quantile body condition index presented here (BCI $_{\text{bill length}}$) requires only a bill length and mass measurement in the field. Those measurements are already frequently collected in the field. Thus, the index could be a useful tool for further research. The preliminary explorations into the variation of adult BCI $_{\text{bill length}}$ at Robben Island indicated that body condition did not differ significantly between the months and years of the study (Fig. 3.12). This finding was contrary to our expectation of a decline in body condition of adults provisioning for small chicks over the breeding season. A purse-seine closure was in place during all years of the study and could possibly explain the consistency observed. However, this would need to be investigated with measurements of breeding adults at times outside of the closure and it is possible that an effect could be masked by other environmental conditions.

All African Penguins sampled in the foraging study were at the same stage of breeding, provisioning for small chicks. It is likely that penguins have to be in a minimum body condition in order to invest in raising chicks and that could explain the uniformity in body condition that was observed. Even though this requires further investigation, this exploratory example indicates that BCI $_{\text{bill length}}$ is a useful tool for monitoring body condition of breeding African Penguins at colony.

Release criteria

The variability in structural size of the African Penguin is sufficiently large that it is inappropriate, for this species, to simply use body mass as an indicator of body condition. The measurements of adults between the 5% and 95% quantile lines show a wide range of sizes for birds obtaining the body mass criteria of 2.8 kg and above (Fig. 3.1). The calculations of BCI for the birds released from SANCCOB showed that a few birds were below average body mass for their size even though they had all obtained the release criterion body mass of 2.8 kg (Fig. 3.13). The mass-based release criteria likely creates a sex bias in captivity time and the condition of birds released because females would be kept longer than males. Such longer treatment times of females might be a factor in the higher mortality of females in captivity (Pichegru and Parsons 2014).

Incorporating BCI $_{\text{bill length}}$ could improve release criteria because it provides more information than body mass alone. Use of the BCI could facilitate identification of healthy body masses and avoid releasing large birds at low body mass for their size and keeping small birds in captivity longer than is necessary. In this way, the BCI $_{\text{bill length}}$ would likely minimise a sex bias in captivity times or body condition at release. Adults in rehabilitation with BCI $_{\text{bill length}}$ of one or greater may be overweight birds. African Penguins can fatten in captivity as they are hand-fed and do not obtain the equivalent amount of exercise in rehabilitation than they would at sea (Nola Parsons pers. comm.). An adult body condition index could provide additional information to rehabilitation centres for identifying when African Penguins in rehabilitation obtain a healthy body mass for their size which could potentially improve chances of survival upon release.

Captivity entails various sources of stress (Morgan and Tromborg 2007) and it is not known if chronic stress persists after capture in captivity in African Penguins and, if so, how long it takes to dampen. The nature of stress physiology in the transfer of wild birds into captivity has been examined in detail with Chukar (*Alectoris chukar*), where stress physiology by the hypothalamic-pituitary-adrenal (HPA) axis dampens corticosterone, an acute stress hormone, after 9 days in captivity (Dickens et al. 2009). However, the timing is likely variable for different species (Dickens et al. 2009). Besides potentially minimising chronic stress, there are other health advantages to minimising the length of time wild African Penguins are kept in captivity such as minimizing disruption to life-history phases and exposure to disease (Parsons and Underhill 2005).

Further considerations of the quantile approach and adult BCI $_{bill\ length}$

Identifying penguins that are in low body condition in relation to their size with the BCI $_{\text{bill length}}$ allows for causes to then be investigated. There are many factors that are likely to affect the body condition of an African Penguin such as stress hormone levels, parasite loads, injury and disease. There are a variety of indicators that can be used as proxies for seabird health besides external morphometrics that are non-destructive such as sampling feathers, blood, excreta and eggshell (Mallory et al. 2010). Such samples can be used to provide insight on contaminant levels (Yin et al. 2008, Bouwman et al. 2015), nutrition with stable isotopes (Cherel et al. 2005), and into hormones and leukocyte profiles (Vleck & Vleck 2002) with which colonies and populations can be compared.

It is important for body condition indices to account adequately for variation across body sizes and for investigators to be aware of index assumptions to avoid misinterpretation of data (Jakob et al. 1996) and spurious results (Green 2001). The quantile body condition index approach is likely to have similar caveats to the use of residuals from regressions of a body mass against a body structure indicator outlined by Green (2001), in that it will not be completely independent of body mass and one size variable may not be fully indicative of structural size. Nevertheless, this approach has advantages over using residuals of a regression or a scaled-mass index: it can account for heteroscedasticity in the data and it is easy to understand conceptually and interpret biologically. A comparative measure makes more biological sense than a size adjusted body mass such as the scaled mass index described by Peig and Green (2009). A mass independent of an animal's size is purely theoretical whereas the comparison of an animal's body mass in relation to other animals of that size can be easy to interpret.

Quantile body condition indices such as the one presented here, could be developed for other species. It could be particularly helpful in species where although measurements are limited, substantial numbers of birds have been (or can be) measured. In the case of the African Penguin handling time is minimised so generally only a few morphological measures are collected in the field. Thus, the index was developed using mass and only one size measurement. However, if a larger number of measurements are feasible, then these measurements can be reduced to a single size measurement by using, in place of bill length (or other size variable) the first principal component. Such an approach is in use by Hood et al.(1998); where the first principal component of a matrix based on four measurements of Magellanic

Penguins (bill length, bill depth, flipper length and foot length) is regressed against body mass and the residuals from the regression are used as the body condition index. A principal component analysis approach could be used with quantile regression should more size variables be available. However, it is not appropriate approach in the case of the African Penguin. The quantile body condition index approach presented could likely be applied to other species and in particular in the cases where measurements are limited, yet a substantial number of birds have been or can be measured. The $BCI_{\text{bill length}}$ could potentially be applied to other seabirds and taxa. The main strengths of the $BCI_{\text{bill length}}$ presented which uses a quantile approach are its ability to account for heteroscedasticity in the data and the ease of biological interpretation.

Conclusions

The body condition index presented here for adult African Penguins, based on quantile regression, is a tool that allows us to obtain a good indication of the physical status of a penguin using only two measurements. It can also be used to improve release criteria at rehabilitation centres and, as a consequence, could increase adult African Penguin survival rates after rehabilitation. This tool has the potential to address some of the knowledge gaps for the species such as comparing the relative body condition of adults spatially and temporally. It could be used to investigate relationships between body condition and behaviour.

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Chapter 4

Foraging behaviour of African Penguins provisioning chicks at Robben Island

Tracking a seabird species at risk when rearing chicks can inform conservation by identifying their habitat requirements at-sea during reproduction and by identify drivers of foraging behaviour. Endangered African Penguins (*Spheniscus demersus*) provisioning chicks were tracked using GPS temperature depth devices when a purse-seine closure areas out to 20 km radius around the Robben Island colony was in place, from 2011 to 2013. This provided an opportunity to see how behaviour varies between and within-years without the confounding factor of local fishing. Foraging areas were identified using kernel density analysis. Intrinsic and extrinsic factors other than prey are considered in this chapter. PCA variable factor maps were plotted to explore relationships between supplementary variables of interest and foraging behaviour measures. Linear regressions were conducted with significant correlations. The median foraging distance from the colony was 9.5 km but foraging was also observed at distances > 50 km. Annual differences were identified in GPS tracks and dive behaviour but the area within 20 km from the island had consistent use. Foraging areas and behaviour of the sexes were comparable. Brood mass at deployment explained almost a quarter of the variation in the time diving. Wave conditions had weak negative correlations to foraging distance and the number of dives but were unable to explain the variation in those behaviours. Annual differences in foraging behaviour were not explained by penguin body mass, size, condition, brood mass, or wave conditions.

Introduction

The foraging effort which adult African Penguins (*Spheniscus demersus*) put into provisioning for their chicks is considered an important component to understanding the ecological dynamics of this species (Sherley 2010, Weller et al. 2014). Advances in logger technology have greatly improved the scope of seabird investigations; tracking can provide information on foraging behaviour (Weimerskirch et al. 2002, Mattern et al. 2007, Guilford et al. 2008, Steinfurth et al. 2008, Kotzerka et al. 2010), responses to anthropogenic pressures (Votier et al. 2010, Bertrand et al. 2012) and identifying sex-specific differences (Lewis et al. 2002, Weimerskirch et al. 2006, Ludynia et al. 2013, Pichegru et al. 2013). In addition, GPS devices in combination with time depth recorders can provide detailed data-rich information of the bird's dive behaviour and thus help to derive a three-dimensional view of the species' movement at sea (Burger and Shaffer 2008). In penguins, studies have shown that time depth data can provide proxies of feeding events (Simeone and Wilson 2003, Bost et al. 2007, Hanuise et al. 2010, Sala et al. 2012). Improving comprehension of foraging behaviour will inform conservation management for this endangered species (BirdLife International 2013, Government Gazette of South Africa 2013).

Parental care is shared in the African Penguin, when chicks are small one parent stays at the nest while the other forages at sea (Wilson 1985; Wilson & Wilson 1990). When provisioning chicks African Penguin foraging behaviour is more regular allowing for researchers to be equip them with devices that require retrieval (Nagy et al. 1984, Wilson and Bain 1984a, 1984b). This has allowed for studies on the foraging behaviour of chick-rearing African Penguins in the Western Cape in the southern Benguela (Nagy et al. 1984, Wilson and Bain 1984a, 1984b, Wilson 1985a, 1985b, Wilson and Wilson 1995, 1990, Petersen et al. 2006, Pichegru 2008, Pichegru et al. 2009, Waller 2011), in the Eastern Cape in the Agulhas ecosystem (Pichegru 2008, Pichegru et al. 2009, 2012, 2013, Wright et al. 2011, van Eeden 2012, Van Eeden et al. 2016), and in Namibia in the northern Benguela (Ludynia 2007, Ludynia et al. 2012b) (Chapter 1, Fig. 1.3). The dive behaviour of African Penguins is known to be similar to that of other *Spheniscus* penguins (Ryan et al. 2007). However, questions remain on the extent different factors influence provisioning behaviour.

African Penguin chick-rearing at the Robben Island colony begins in January with numbers peaking in May and then tailing off in September/October (Crawford et al. 2006, Sherley et al. 2012). Previous sampling of African Penguin chick-rearing foraging behaviour using Global Positioning System-Temperature Depth (GPS-TDlog) devices, has typically taken place during peak chick-rearing times due to logistical constraints, and therefore over short temporal intervals (Petersen et al. 2006, Pichegru et al. 2009, Pichegru et al. 2010, Pichegru et al. 2012, pers. communication with R. J. M. Crawford and A. Steinfurth, unpublished data). This investigation will conduct sampling over several months of the breeding season during years when a purse-seine closure areas out to 20 km radius around the colony was in place to see how behaviour varies between and within-years.

This chapter examines variation in diving behaviour and core foraging areas of chick-rearing African Penguins at Robben Island, a Western Cape colony in the southern Benguela ecosystem. It will also address the relationships of foraging behaviour to intrinsic factors of sex, body condition index, body mass and extrinsic factors of chick brood mass and wave conditions. The findings have implications for species conservation and ecosystem management.

Methods

Ethics

The research was conducted under the auspices of the Oceans and Coasts Branch of the South African Department of Environmental Affairs (DEA). The penguin handling, techniques and monitoring had approval from DEA, the Robben Island Museum and the University of Cape Town Science Faculty Animal Research Ethics Committee.

Data Collection

Data collection took place at Robben Island, a west coast island colony in South Africa in Table Bay, 33°48’S, 18°22’E (Fig. 4.1), in 2011, 2012 and 2013. During these years a purse-seine fishing closure was in place out to a radius of 20 km around the island. The African Penguins breed on the eastern side of the island; this is also the side of the island which is more sheltered and has less wave action (Fig. 4.1).

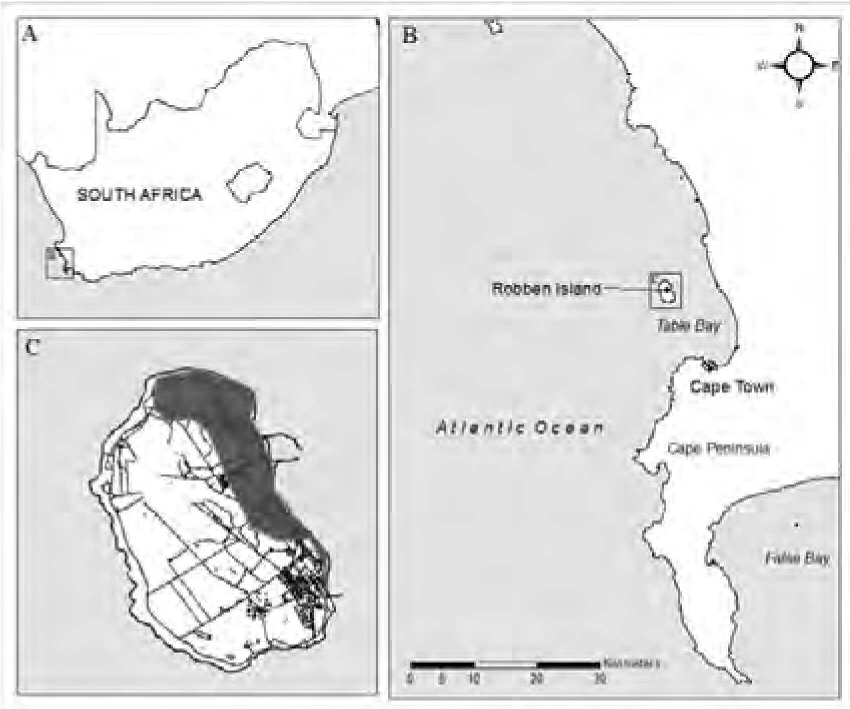


Figure 4.1. Map of (A) South Africa, (B) the area surrounding the Robben Island colony, (C) Robben Island with roads and buildings in black, and areas where African Penguins were breeding in 2011 to 2013 in transparent dark grey

Logger devices

The devices used were Global Positioning System-Temperature Depth logger (GPS-TDlog) devices (Earth&OCEANS Technologies, Kiel, Germany) (Fig. 4.2) or Fastloc 2 loggers (Sirtrack, Hawkes Bay, New Zealand) in combination with a tubular Temperature Depth Recorder (TDR) (Lotek, Newmarket, Canada) (Fig. 4.3). Device dimensions are presented in Table 4.1. GPS-TDlogs were used in 2011 and 2012, while both systems of devices were used in 2013. The GPS-TDlogs were used for 87 of the 90 deployments.

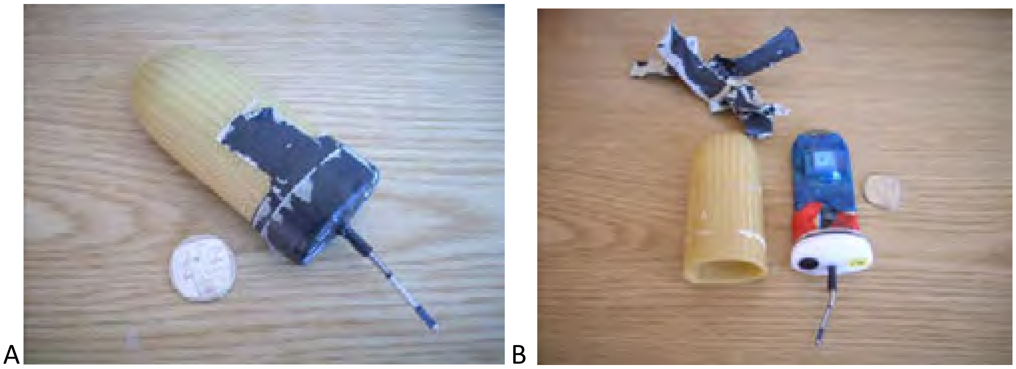


Figure 4.2. The GPS-TDlog device after retrieval shown with a 2 Rand coin which has the diameter of 22 mm for perspective. Photo (A) shows the stream-lined device after retreival with the aramid-fibre composite casing sealed water tight. Photo (B) shows the opened device after the tape is removed, the soldered battery can be seen with red electrical tape coverings and the GPS and programming system are under the plastic blue covering. The temperature sensor is on the probe and the black circle is the pressure sensor, both of which remain exposed during deployments.

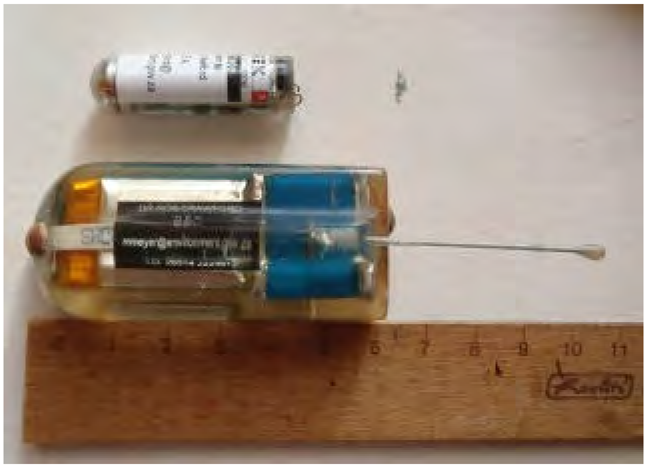


Figure 4.3. The Lotek tubular LAT1800 TDR above and the Fastloc 2 device below. Photo courtesy of Antje Steinfurth.

Table 4.1. The dimensions in terms of length (L), width (W) and height (H) and mass of the logger devices equipped to African Penguins at Robben Island in this study.

Device	Dimension (mm)	Mass (g)
Earth&OCEAN GPS-TDlog	L × W × H: 100 × 48 × 24	75
SIRTRACK Fastloc 2	L × W × H: 69 × 28 × 21	39
Lotek TDR LAT1800 tubular form	W × H: 11 × 38	6

Care needs to be taken when using different devices for several reasons. The programming of data collection needs to be done consistently in ways that are comparable and because devices with differences in cross-sectional area or shape can differ in drag (Culik et al. 1994). Device drag can be influential to behaviour (Wilson et al. 1986, Culik et al. 1994, Ryan et al. 2007). However, energy expenditure of African Penguins with and without devices have been shown to be similar when investigated with doubly labeled water (Nagy et al. 1984, Wilson et al. 1986). Provisioning trips of African Penguins equipped with GPS-TDlog devices have the same trip durations as control birds without devices (Ryan et al. 2004, Petersen et al. 2006, Pichegru et al. 2010). African Penguin mean swimming speeds are related to device size (Wilson et al. 1986) and when devices are large they can affect the amount of prey and energy needed for the penguin to sustain itself and whether there is an excess available for its chicks (Wilson et al. 1986). Survival probabilities of chicks in the foraging study were comparable to those of control chicks (Chapter 7).

The accuracy of both GPS devices is dependent on the number of satellites detected (Ryan et al. 2004, Dujon et al. 2014). Efforts were made to program the devices using comparable intermittent modes. Both devices recorded geographical position using the standard World Geodetic System (WGS) 1984. In order for the devices to record for the duration of an entire foraging trip, the GPS-TDlog devices were programmed to record one geographical position per minute or upon each surfacing, while the Fastloc2 loggers were programmed to record a GPS position every 2 minutes only when the bird was at the water surface. Intermittent GPS modes with GPS-TDlog devices are known to be accurate to less than 10 m for 68% of fixes and less than 20 m for 90% of fixes (Ryan et al. 2004). Temperature and pressure data were recorded every second. Both devices had up to 12 bit data resolution and measured temperature to better than 1°C (earth&OCEAN Technologies 2009, Lotek Wireless Inc 2011). The GPS-TDlog pressure sensor measured from 0–20 bar and use of this pressure range provides a depth resolution of ca. 5 cm in the water column (earth&OCEAN Technologies 2009). The Lotek TDR device measured pressure resolution to 0.05% (Lotek Wireless Inc 2011), in our case this translates to a resolution in the water column of ca. 2.5 cm (pers. comm. with a Lotek representative).

The larger GPS-TDlog devices used the majority of the time approximately a 7% sectional area of an African Penguin (Ryan et al. 2007). The Tesa^{TM} tape (10 mm-wide strip Tesa-Tape Nr. 4651, Beiersdorf AG, Germany) used for attachment (details in section “*Device deployment and retrieval”* below) weighed up to 2 g when wet. So devices with tape weighed at most 77 g, this mass is less than 4% of the weight of the smallest penguin equipped with a logger (2 kg), and on average was < 3% of the bird’s body weight. For diving species that do not fly, the effect of drag from the device shape and size is of greater concern than device weight (Bannasch et al. 1994). For this reason devices were carefully positioned on the dorsal line of the bird's lower back (details below).

Selection of study individuals

The African Penguin is an endangered species (BirdLife International 2013). It was imperative for ethical reasons that the research not harm the study animals or hinder their breeding attempts. Deployments were made on one of the adults of a pair at a nest and only once during a breeding season. Selected individuals were equipped with a device for one foraging trip. Study individuals were carefully selected to reduce the stress and costs of the deployment to the individual and also to minimise the probability of nest abandonment or failure. Selections were based on penguin behaviour and nest type.

Nests were selected where adults were alternating chick brooding and foraging on a daily basis, sharing parental care evenly. During nest visits prior to deployment if an adult displayed signs of stress such as trembling, fled the nest site or made repeated aggressive vocalisations, described in detail in Favaro et al. (2014) as agonistic calls, it was excluded from the study and not equipped with a device. I interpreted these visual and auditory cues to indicate stressed birds. However, this assumption requires further physiological investigation. There are a variety of nest types on Robben Island both natural and artificial (Table 1.2). When nest boxes were available they were chosen in preference to natural nests because their structure made it easier to remove adults from the nest, reducing capture time and preventing birds from fleeing when returned to the nest box. In the case of burrow nest types, penguins often dug their nests deeper after deployments making capture time longer than at nest boxes. Natural nests which were overhung by low branches were avoided to prevent devices becoming entangled upon the bird's nest exit or re-entry. Nest type was noted because artificial nests have a greater breeding success on Robben Island than nests under vegetation (Sherley et al. 2012).

Individuals selected had to be without flipper bands. At the time the study took place, African Penguins were not being individually marked. During the study, birds were temporarily marked with a non-permanent animal marker (Porcimark^{TM}, Kruuse, Langeskov, Denmark) to distinguish partners from each other. Photos were taken of spot patterns; these are unique and aid subsequent identification (Sherley et al. 2010).

Adults with small chicks were selected because their at-sea foraging behaviour is regular and generally under 24 hours (Wilson and Wilson 1990), so device batteries would last long enough to record an entire foraging trip. When chicks grow larger, food demands are higher and adults spend longer at sea and start leaving the chicks unguarded (Wilson et al. 1989, Wilson and Wilson 1990, Seddon and van Heezik 1993). To be assured of device retrieval, African Penguins provisioning small chicks classified as P1/P2 , in the guard stage, were selected to be equipped with devices (Fig. 1.5). In 2011 and 2012 deployments were conducted throughout the breeding season when there were appropriately sized chicks. Due to logistical constraints in 2013, deployments were only conducted during peak breeding season in May and June.

Device deployment and retrieval

For device deployment, selected adult penguins were captured by hand at their nest while brooding chicks. A firm grip on the bird's head had to be maintained and the body weight supported during all capture and handling. Keeping the bird immobile and always properly supported during the deployment was necessary to prevent the bird from struggling which can increase stress as well as the chances of the bird behaving in an atypical manner (Wilson 1997). Deployments and retreivals were always conducted with an assistant to hold the penguin while the device was fitted or removed. During device attachments and retrievals, penguins were held immobile and their heads were covered with a cloth to obscure their field of vision because these procedures reduce the stress of handling (Wilson 1997, Wilson and McMahon 2006).

Devices were mounted at the midline on the most caudal position of the bird's back because this positioning causes the least amount of drag from devices (Bannasch et al. 1994). The devices were attached with overlapping layers of black waterproof Tesa$^{\text{TM}}$ tape which matched the birds' plumage in colour and did not compromise feather structure (Wilson and Wilson 1989, Wilson et al. 1997). The method of attachment was that recommended for short-term attachments by Wilson et al. (1997); for further details of procedures see Ludynia (2007). One person held the bird while another attached the device to minimize handling time. The nest was watched during deployment to make sure chicks did not leave the nest site in the absence of the adult. Once equipped, the adult was returned to its nest and chicks.

Nest visits were conducted at least once per day after logger deployment, to determine whether the equipped bird went to sea and to retrieve the device upon the bird's return to the nest. If a bird did not return to the nest after a day being absent (presumably at sea) then multiple nest checks were made the next day. If a bird was not present for two days, night checks were conducted because both partners were often found at the nest at night. All devices were retrieved successfully. To retrieve the device, the bird was once again removed from its nest and the head covered with a cloth. The Tesa^{TM} tape was removed from the device following Ludynia (2007). First the device and then the remaining tape was removed gently and quickly from the bird's back feathers. Morphometric measurements of the equipped bird were taken at device retrieval. To identify the sex of the bird, the bird's bill length and depth following Cooper (1972) were measured with callipers to 0.1 mm (Chapter 2: Fig. 2.2). In 2012, a bill depth measurement at the base of the bill was additionally taken following Pichegru et al. (2013) (Chapter 2: Fig. 2.2). Adult birds were weighed with a harness and a digital scale Rapala^{TM} to the nearest 0.01 kg.

Measurement of partner and chicks

The adult of the pair that was not equipped with a device was termed the partner bird. Both birds of the pair were measured to determine sex of the birds equipped with devices. Chicks were weighed in a cloth bag to the nearest 0.01 kg and head length was measured with callipers to the nearest 0.1 mm. Initially, partners and chicks were measured the day after the deployment when the equipped bird was at sea. However, following concerns after penguins were observed moving nest site after the partner and chick measurements took place (occurred 4 times) those measurements were conducted following retrieval to avoid nest disturbance prior to the equipped bird's return. In this way there was less disturbance during the period the equipped bird was absent from the nest. Typically, partner and chick measurements took place on the day following retrieval but in some cases measurements were made later due to weather conditions, adult penguins being absent from the nest or logistics. On occasion, the equipped bird brooded the chicks for more than one day following the retrieval. In a few cases, the partner birds were not observed on subsequent visits; it is possible that birds were visiting chicks at night but night checks were not made to obtain partner measurements due to logistical constraints.

Sexing adults

I first tried to sex the penguins using the partner measurement comparison method following (Duffy 1987), in which the male of a pair is identified by the larger bill depth and length. However, in many cases both measurements were not both larger for one penguin of the pair. In those cases the male was determined by a comparison of Farah discriminant function scores (Chapter 2) and the bird of the pair with the larger score was considered the male. In the case that the partner's measurements were unknown, the Farah discriminant function was used to identify sex and the cutpoints were used to avoid misclassifying birds. This approach meant some birds remained unsexed.

Environmental data

Bathymetry around Robben Island was provided by the South African Navy Hydrographic Office, Republic of South Africa. Wave data were collected at Cape Point wave buoy (34°12'14.40"S, 18°17'12.01"E) at a distance of 5.4 km from the coast and 43.3 km south-east of Robben Island by the Council for Scientific and Industrial Research (CSIR). They provided the hourly wave height and direction for all the hours that African Penguins were at sea with devices.

Analysis

GPS track analysis

In all cases, outlier GPS error points on land and outliers at sea were removed. The foraging effort measures of foraging distance, path length (km), trip duration (h), and time spent away from nest (h) were derived from the GPS data (Table 4.2). The GPS tracks were mapped in ArGIS ArcMAP version 10.2 (ESRI). Tracks were also mapped in GoogleEarth with GPS points connected with straight lines for visualisation aids of typical behaviours. Inter-annual differences in measurement distributions were examined with Kruskal-Wallis tests because distributions of these measures were non-normal, and followed by post-hoc Dunn's tests where appropriate. In cases where multiple foraging trips were recorded by the same individual, only the first trip was included in the analysis to avoid pseudo-replication.

Pearson's product moment correlation coefficients were calculated between foraging distance, path length and trip duration, the most commonly presented parameters for at-sea track data for the species (Petersen et al. 2006, Ludynia 2007, Pichegru et al. 2009, 2010, 2012, 2013, Ludynia et al. 2012b) to test for correlations. Foraging parameters were plotted over time annually and monthly to explore inter- and intra-annual variation, respectively.

Table 4.2. Foraging trip behaviour measures and their definitions investigated in this study for the African Penguins equipped with devices at Robben Island.

Measure	Description
Foraging distance (km)	Straight line distance from Robben Island where bird entered the sea to the furthest trip point
Path length (km)	Total distance travelled during one foraging trip when at sea
Duration (h)	Foraging trip duration is the total time spent at sea, calculated from when the bird entered the sea to when it returned to the island
Duration away from nest (h)	Time spent away from nest
Dive depth (m)	Depth at the deepest part of a dive
Dive duration (s)	Total duration of a dive
Post dive intervals (s)	Time between the end of a dive and the start of the next dive

No. Dives	Sum of the number of dives. Dives were considered to have occurred at depths > 1 m
No. Foraging dives	Sum of the number of potential foraging dives where the dive depth was > 3 m
Time diving (h)	Sum of the dive durations
Diving frequency (dives h^{-1})	Number of dives per trip divided by the trip duration in hours
Time diving (%)	Time diving (h) of the total time at sea (h) multiplied by 100
Vertical distance (km)	Sum of the maximum dive depths multiplied by two
Wiggle	A pattern in the dive profile of an inflection point followed by a maxima followed by another inflection point where the mean change in depth had to be > 0.3 m over one second and had to be more than the mean rate of change over the previous three seconds
Catch per unit effort (CPUE)	Total number of wiggles of a trip divided by the total bottom phase time in minutes

Dive data analysis

When travelling African Penguins remain within three meters of the surface (Wilson and Wilson 1990) and dives deeper than 3 m can be considered possible foraging dives (Wilson and Wilson 1990, Pichegru et al. 2010). Dive data were analysed using MTDive (Jensen Software Systems, Laboe, Germany). The dive threshhold was set at > 1 m depth to include travelling dives but exclude noise from wave action or and noise when birds were at the water surface. Thus dives deeper than 1 m were selected for further analysis. I checked the selection of each dive by the MTDive software for pressure anomalies. Dives were classified into descent, bottom and ascent phases and the period in between dives was the post-dive interval (also known as a post-dive pause) (Fig. 4.4). The bottom phase was identified using the 'normal kind' searching bottom phase setting in MTDive. The bottom phase was considered to be bound by two points of inflection, having an overall rate of change of depth that did not exceed 0.25 m/s (Kato et al. 2006, Pichegru et al. 2011, Sala et al. 2012). The slimness, the ratio between the duration at the bottom two thirds of the maximum dive depth and the entire dive duration was set at 0.5, the recommended default setting. Slimness concerns the detection of V or U shaped dives and hence bottom phase detection. Further details of dive analysis parameters used can be found in Supplementary Materials S1. The details of each selected dive were then extracted into an output Excel file by MTDive for further analysis.

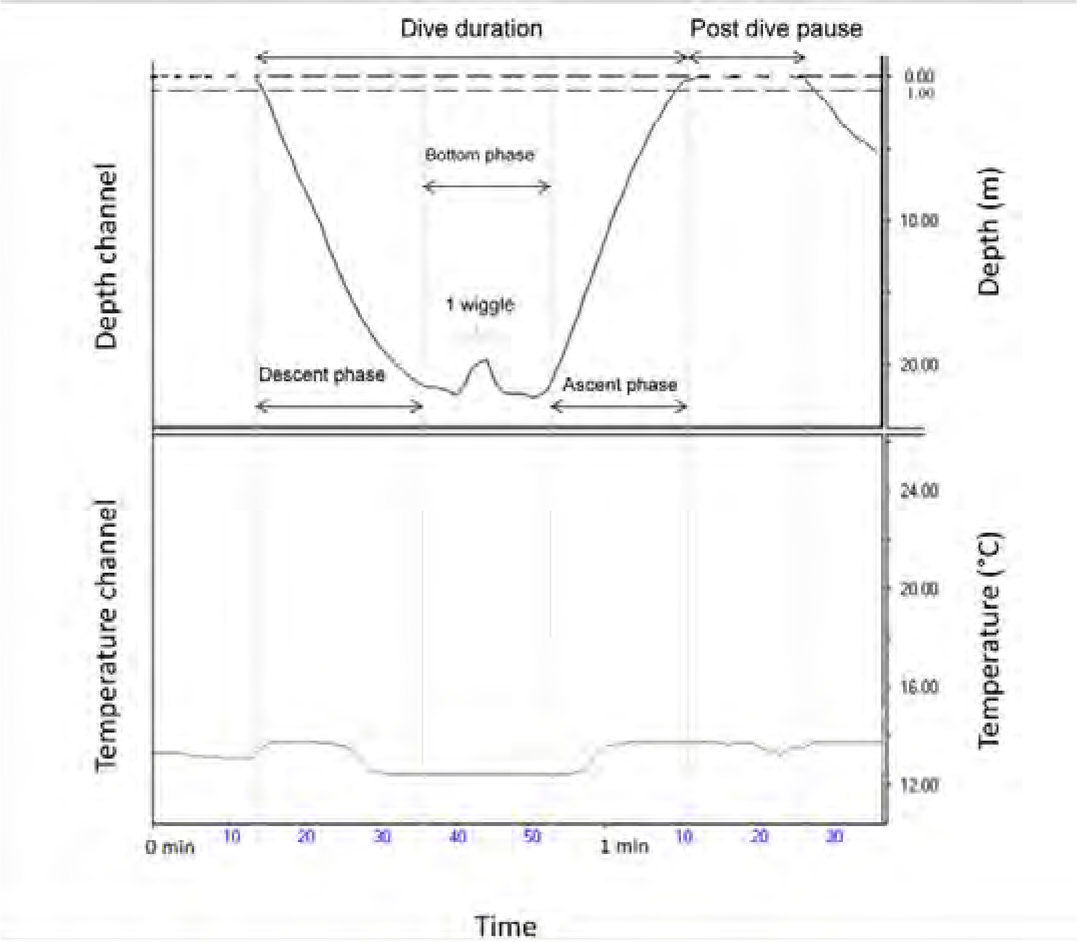


Figure 4.4. Illustration of dive phases with an example of an African Penguin dive.

Dive parameters were calculated for all complete dive data sets (Table 4.2). Dive efficiency (DE) was also calculated as bottom duration divided by the dive duration and post-dive interval for all dives with a post-dive interval, as in Zimmer et al. (2010b)following the equation:

$$\mathrm{DE} = \frac{\text{bottom phase duration}}{(\text{dive duration}+\text{post dive interval})} \qquad \text{(Eqn. 4.1)}$$

To avoid bias from the long post-dive intervals I compared the median DE values for each penguin because medians are robust to outliers.

Wiggles as a proxy for prey capture

Wiggles, also known as undulations, have been rigorously investigated as indicators for prey capture and feeding events in Magellanic Penguins (*S. magellanicus*) (Simeone and Wilson 2003, Sala et al. 2012), Adélie Penguins (*Pygoscelis adeliae*) (Bost et al. 2007) and King Penguins (*Aptenodytes patagonicus*) (Bost et al. 2007, Hanuise et al. 2010). The application of wiggles as a proxy for prey capture in other *Spheniscus* penguins is recommended (Simeone and Wilson 2003).The Magellanic Penguin is the closest relative of the African Penguin (Ksepka et al. 2006) and their dive behaviour is similar (Ryan et al. 2007). Therefore, it is likely that vertical displacement or dive behaviour in prey pursuit would be similar.

Simeone and Wilson (2003) defined wiggles to be a change in depth over a second that is > 0.3 m more than the mean rate of change of depth recorded over the previous three seconds, unless a wiggle already began within that time step. The particular change in depth was chosen because it is roughly twice the maximum ventro-dorsal diameter of a Magellanic Penguin. Twice the maximum ventro-dorsal diameter of an African Penguin would also be roughly 0.3 m. Halsey et al. (2007) further explained wiggles as a particular pattern in the dive profile in which an increase in depth over time changes to a decrease in depth and then back to an increase in depth. Here, I incorporate the two definitions of Simeone and Wilson (2003) and Halsey et al. (2007) and define a wiggle to be an inflection point followed by a turning point that is a maxima and another inflection point (Fig. 4.5). For the African Penguin using the change in depth over the time window suggested by Simeone and Wilson (2003) for Magellanic Penguins seems the most appropriate (Table 4.2). A wiggle is defined as a pattern of an inflection point a maxima and another inflection point in the bottom phase where the mean change in depth had to be > 0.3 m over one second and had to be more than the mean rate of change over the previous three seconds. This definition was used to analyse the dive data with MTDive software.

To estimate the catch per unit effort (CPUE), the total number of wiggles per foraging trip for each penguin was divided by the total time the penguin spent in the bottom phase in minutes. This provided an estimate of prey ingestion rate.

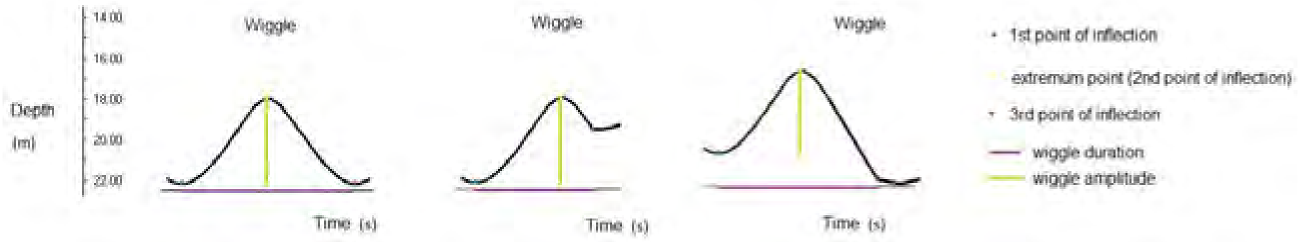


Figure 4.5. Three schematic drawings as examples of wiggles or undulations in the dive profile. A wiggle is characterised by a pattern in the dive profile of an inflection point followed by a maxima followed by another inflection point. This was further restricted for the African Penguin, as it is with the Magellanic Penguin (Simeone and Wilson 2003), to where the mean change in depth had to be > 0.3 m over one second and had to be more than the mean rate of change over the previous three seconds.

Inter-annual comparisons in dive behaviour

Some of the dive behaviour measures had multiple values for each individual. This was the case for dive depths, dive durations, phase durations and DE. For these measurements, linear mixed effects models were used to investigate inter-annual and sex differences using the 'lme' function in the 'nlme' R package (Pinheiro et al. 2014). Year and sex were fixed effects while bird identity was used as a random effect. The models were fitted using restricted maximum likelihood REML. Plots of the residuals were examined to check the assumptions of residual normality and homogeneity of variance were met. In the case of DE, removing the values associated with long post-dive intervals gave similar results as models with all the data so I chose to present the analysis with all DE values.

Interpolation of foraging dives

Both the GPS and dive data sets were used in combination to identify the spatial locations of foraging dives. One incomplete track was included in which the battery failed on the penguin's commute return to the colony, to make use of all observed at-sea foraging areas. This made the total sample from 75 penguins. A linear interpolation was used to identify the foraging dive locations. Dives associated with GPS gaps of 20 minutes or more were cut to avoid inaccurate interpolations. The value of 20 minutes was chosen by examining a histogram of all the GPS gaps intervals; it allowed for 77% of the GPS data to be retained. Any dives interpolated as being on land were removed as they were clearly erroneous.

Total area, core area and home range of foraging

The total foraging area used by chick-rearing penguins was estimated with 100% minimum convex polygons (MCP) for the interpolated foraging dives calculated for each year, using the Geospatial Modelling Environment (GME) 'genmcp' function (Generate Minimum Convex Polygon) and then mapped in ArcGIS 10.2. The core foraging area and foraging range area were identified by kernel density estimation for foraging dives using the Geospatial Modelling Environment (GME) (Beyer 2015) with a bandwidth of1 km, a cell size of 1 km, and a quartic distribution for the kernel type because this closely corresponds to a real distance on the ground with the 'kde' function (Kernel Density Estimation). The smoothing bandwidth of 1 km was chosen because such a bandwidth is comparable to a gridded overlap approach (Tancell et al. 2013). This produced kernel density raster files from which I created isopleths for the percentage volume contours of interest with the GME function 'isopleth' (Isopleths). The 50% volume contour was used to identify the core foraging area and the 90% volume contour for the foraging home range. Polygons were then created from the isopleth lines in ArcMAP. The core foraging areas and home range areas for all three years of foraging dives were generated separately and then together. Core foraging areas were also conducted for the data collected monthly. For the core foraging area and home range area of combined years the bathymetry contour lines were overlaid to provide further context to those marine environments.

Spatial foraging comparison of the sexes

The 100% MCPs were generated for the foraging dives of all sexed individuals, and the sexes separately, as described above. The areas of each MCP and area overlap were calculated in ArcMap 10.2. This method is sensitive to extreme points or individuals and can incorporate large areas that are not used (Anderson 1982, Powell 2000, Girard et al. 2002). In an attempt to address this, I investigated the foraging area covered on an individual basis with MCPs. Then, I tested for differences in the foraging area used by males and females with Mann Whitney *U*-tests.

Data were collected over several months so there was concern that environmental conditions at different times could bias findings. Furthermore, sampling of males and females was not even because sex was unknown at the time of device deployment. To address these concerns and explore whether there were spatial differences in foraging between the sexes, I blocked by month nested in year in that I randomly selected even numbers of males and females for each month sampled. In this way variability due to environmental conditions was minimised. Tests between the foraging areas of the sexes were conducted using Student's *t*-test.

Wave conditions analysis

For the period a penguin was at-sea, the mean wave height was calculated from the hourly wave height data (m). Mean wave direction was calculated from the hourly wave directions over the hours of the foraging trip. Wave direction is the direction the waves are coming from in degrees clockwise from true north. Wave direction was investigated with circular statistics. The mean wave conditions experienced by equipped penguins were compared between years.

Exploration of intrinsic and extrinsic factors on foraging behaviour

Principal component analysis (PCA) is a recommended approach to identify factors influential to foraging behaviour measures (Zimmer et al. 2010a). The foraging behavioural measures were chosen following Zimmer et al. (2010a), for comparison sake and also because none of them were tightly correlated, these were: foraging distance from the colony, total time diving, median dive depth, number of dives, mean bottom phase duration, and total number of wiggles. I combined data of the sexes and all years because otherwise sample sizes were small and findings could be spurious artefacts of small sample size. PCAs were performed in R with the 'PCA' function in FactoMineR package (Husson et al. 2015).

Supplementary variables of interest were added to the PCA of foraging measures separately to identify any strong relationships. The influence of the intrinsic factors investigated were bird structural size using bill length (mm) and an adult body condition index (BCI) presented in Chapter 3. Whether these varied between years was examined with ANOVA because sample sizes were small, prior to conducting the PCA. The extrinsic explanatory factors were brood mass, mean wave height and mean wave direction. They were investigated in the same way. Brood mass was measured at deployment in some cases and after deployments after a change in protocol so it was analysed at different timeframes separately where sample sizes allowed. I looked at whether foraging behavioural measures were related to brood mass at deployment and brood mass measured two days from the day the equipped bird was at-sea. Sample sizes were too small to test for differences between years for both groups. Samples of brood mass measured within two days of the equipped bird being at-sea were large enough for differences between years to be tested with ANOVA.

PCA variable factor maps were plotted to assist in identification of relationships between each supplementary variable of interest and the foraging behaviour measures (following Zimmer et al. 2010a). The greater the strength of the relationship of the variable of interest to foraging parameters, the longer the factor arrow of the supplementary variable of interest. A variable of interest with a small factor arrow would indicate weak relation with foraging parameters. The lack of an arrow for the supplementary variable of interest would indicate no relation with the foraging parameters. Factors are positively correlated when the angle between them is small, < 45°. Factors are negatively correlated when the angle between them is large, > 135°. Factor arrows with zero degree rotation indicate a correlation of +1. Factor arrows with 90° rotation indicate no relation. Factors with arrows which are 180° to each other indicate negative correlation of -1. For factors that appeared related subsequent correlation tests and regressions were conducted.

Statistics

All statistics were conducted in R (R Core Team 2013). The circular statistics were analysed with the R package 'circular' (Agostinelli and Lund 2013). For between-years comparisons when samples sizes were small, less than 30, ANOVA were conducted. In those cases, standard error was presented instead of standard deviations because there is uncertainty of the distributions of the data. Where distributions were non-normal, non-parametric tests were conducted and data were summarised with median and range.

Results

Tracks were collected from May to August in 2011, April to August in 2012 and May to June in 2013. Deployments were made on 90 birds in total: 32 in 2011, 42 in 2012 and 16 in 2013. All devices were retrieved successfully. In three cases, the devices were removed before the penguins went to sea because the penguins stayed at their nest longer than usual and the device battery would not last for an entire foraging trip. Dive data was collected from 75 penguins. GPS data was collected from 78 penguins in total but complete tracks of the foraging trip were recorded from 71 penguins. The devices yielded complete data sets, recording over an entire foraging trip, for both dive and GPS 82% of the time (71 out of the 87 times devices were deployed and went to sea) (Table 4.3). Chicks were estimated to be on average 16.5 days old at the date of deployment using developmental characteristics, nest monitoring and nest-days calculated using Mayfield methods(Mayfield 1975). Partner and chick handling time including capture was on average 6 minutes. Handling during device deployment took on average 10 minutes while retrieval and measurements took on average 6 minutes, both including capture time.

Table 4.3. Sample sizes of chick-rearing African Penguins equipped with devices and the number of complete first trip GPS and dive data sets collected in 2011 to 2013 at Robben Island. In a few cases, dive data was collected but not GPS data. The total number of birds is shown as well as the numbers sexed.

	All years				**Year**											
	2011-2013				2011				2012				2013			
Data sets	Total	♀	♂	Sex Unknown	Total	♀	♂	Sex Unknown	Total	♀	♂	Sex Unknown	Total	♀	♂	Sex Unknown
GPS	71	33	34	4	24	15	8	1	35	14	20	1	12	4	6	2
Dive	74	33	37	4	26	16	8	2	37	14	22	1	11	3	7	1

GPS tracking results

The foraging trips of chick-rearing penguins at Robben Island with complete GPS tracks (N = 71) had a median foraging distance from the colony of 9.8 km (range: 3.8–55.6 km), path length of 37.5 km (range: 14.2–259.3 km) and at-sea trip duration of 14.2 h (range: 7.4–59.2 h). The tracks had patterns of the typical behavioural seabird foraging modes of commuting and looping (Weimerskirch 2007) (Fig. 4.6).

Figure 4.6. Foraging track examples of the trips African Penguins at Robben Island made when chick-rearing: (A) two tracks with commute mode patterns, (B) two tracks with looping mode patterns, and (C) two tracks of looping mode patterns with track sections that have a higher increased turning rate.

Foraging track measures differed between the years (Table 4.4). The differences between those measures in 2011 and 2013 were not significant but those years differed significantly from 2012

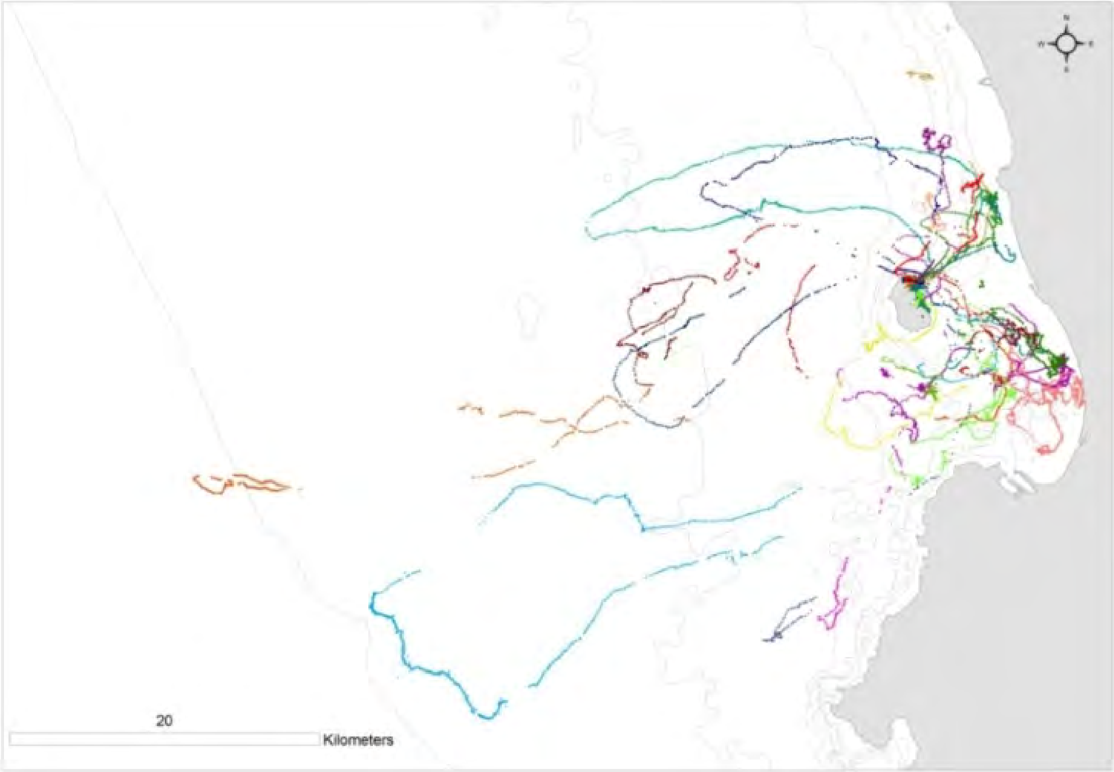
(Table 4.5). In relation to the other two years, in 2012 penguin foraging distance was on average 7.9 km (range: 2.2–40.2 km) closer to the island (Fig. 4.7).

Table 4.4. Inter-annual comparison of foraging trip measures from complete GPS tracking data collected from 71 African Penguins at Robben Island rearing small chicks. Only first trips were analysed to avoid pseudo-replication.

GPS track measures	**Year**			**AVOVA**
	2011 Mean ± SE (range) *N = 24*	**2012** Mean ± SE (range) *N = 35*	**2013** Mean ± SE (range) *N = 12*	Year
Foraging distance (km)	15.5 ± 2.1 (6.0-47.7)	8.9 ± 0.5 (3.8-15.5)	19.6 ± 4.8 (7.3-55.6)	$F_{2,68}$ = 7.3, p = 0.001
Path length (km)	56.1 ± 7.4 (23.2-158.3)	34.3 ± 1.6 (14.2-59.2)	71.8 ± 20.0 (19.2-259.3)	$F_{2,68}$ = 5.95, p = 0.004
Trip duration (h)	16.9 ± 2.2 (8.7-42.9)	11.0 ± 0.5 (7.4-25.4)	19.3 ± 4.5 (9.3-59.2)	$F_{2,68}$ = 4.99, p = 0.009

Table 4.5. Post-hoc Tukey honest significance difference pair comparison results for GPS track measures from 71 African Penguins rearing chicks.

Parameter	Year comparison	Mean difference	95% confidence interval	p-value
Foraging distance (km)	2012-2011	−6.6	−12.4 – −0.7	0.02
	2013-2011	4.1	−3.7 – 11.9	0.43
	2013-2012	10.7	3.3 – 18.1	< 0.001
Path length (km)	2012-2011	−21.9	−44.4 – 0.7	0.06
	2013-2011	15.6	−14.4 – 45.7	0.43
	2013-2012	37.5	9.1 – 65.9	0.01
Trip duration (h)	2012-2011	−5.9	−11.7 – −0.1	0.05
	2013-2011	2.4	−5.4 – 10.2	0.74
	2013-2012	8.3	0.9 – 15.7	0.02



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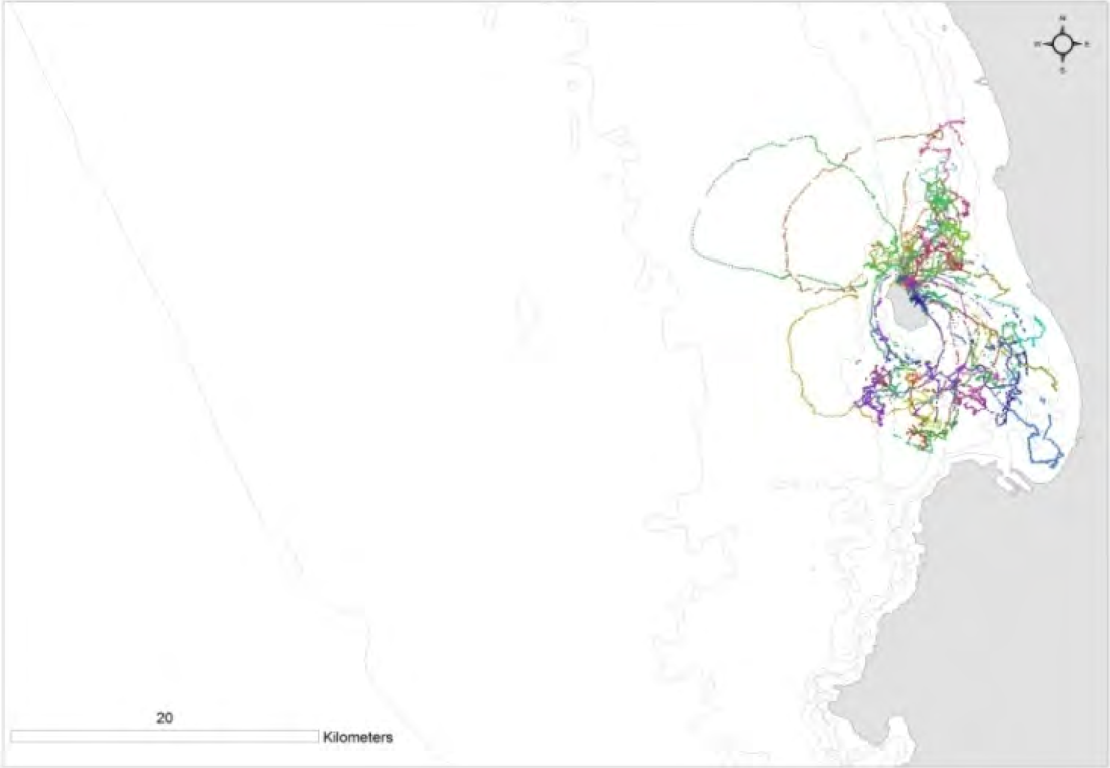

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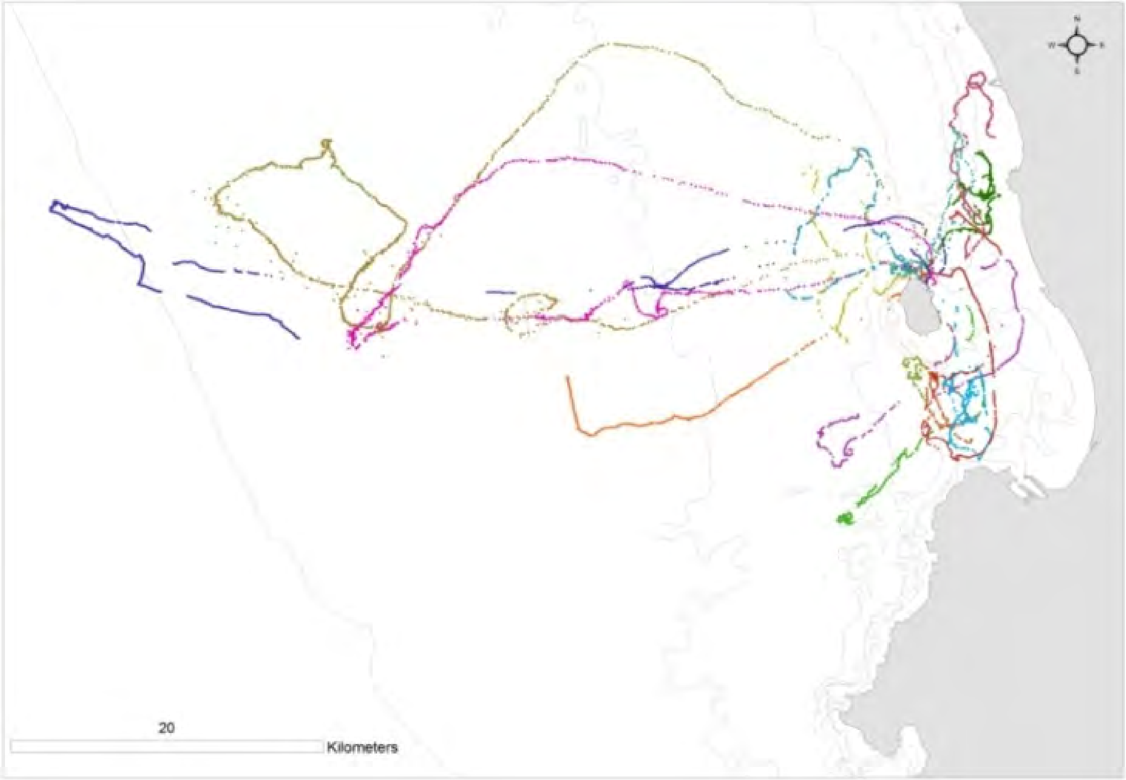
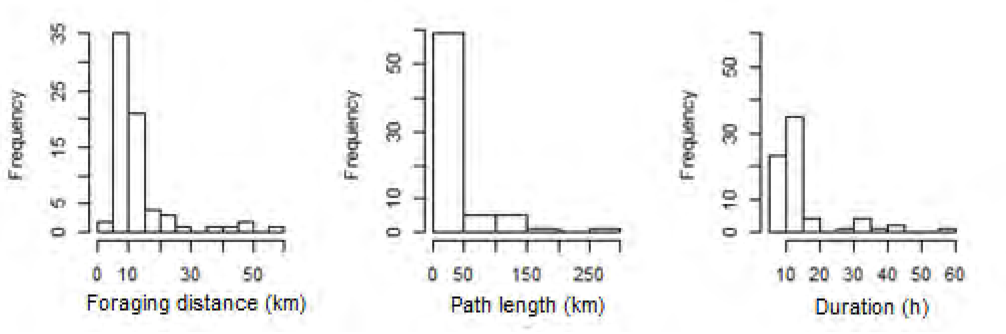


C

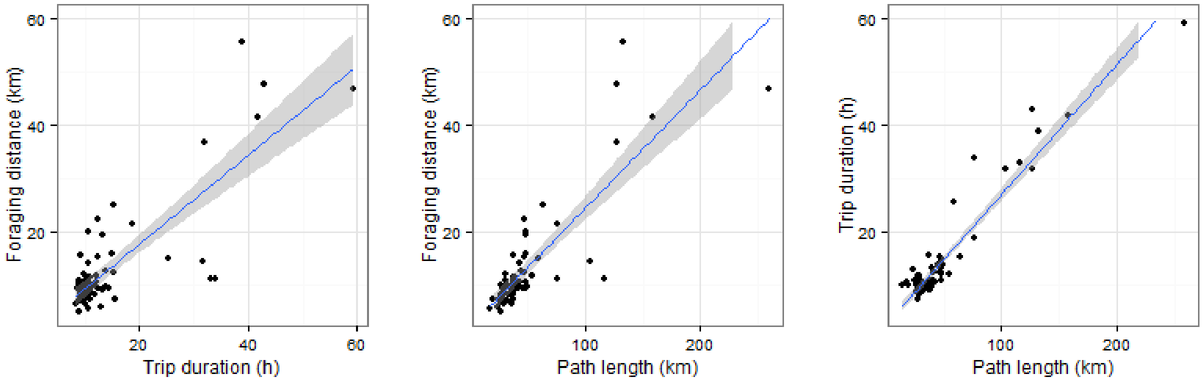
Figure 4.7. Maps of GPS track data (including incomplete tracks) from African Penguins rearing small chicks at Robben Island. Individuals shown in different colours (A) 2011 (N = 26), (B) 2012 (N = 37) and (C) 2013 (N = 15). Isopleths of the bathymetry around Robben Island included in light grey for context.

Combining the data for all years of foraging distance, path length and trip duration indicates that these behavioural measures were uni-modal and skewed to the right by large outliers (Fig. 4.8). The foraging track measures are positively correlated with each other (Fig. 4.9). Thus, further investigation into inter- and intra-annual variation was only conducted on foraging distance. The between year variance in foraging distance was 101.1 km^2 which was higher than the within-year variance in 2012 of 7.3 km^2 but lower than the within-year variance in 2011 and 2013 of 108.4 km^2 and 280.3 km^2, respectively (Fig. 4.10).



A B C

Figure 4.8. Frequency distributions of foraging trip measures from the GPS data: (A) foraging distance, (B) path length and (C) duration from 71 African Penguins chick-rearing at Robben Island, collected in 2011 to 2013.



A B C

Figure 4.9. Scatter plots showing the positive relations between the GPS foraging trip measures of African Penguins rearing small chicks with linear lines of best fit in blue with 95% confidence intervals for (A) foraging distance in relation to trip duration (r = 0.81, t_{69} = 11.6, p < 0.001), (B) foraging distance in relation to path length (r = 0.84, t_{69} = 13.0 , p < 0.001), and (C) trip duration in relation to path length (r = 0.95, t_{69} = 25.5, p < 0.001).

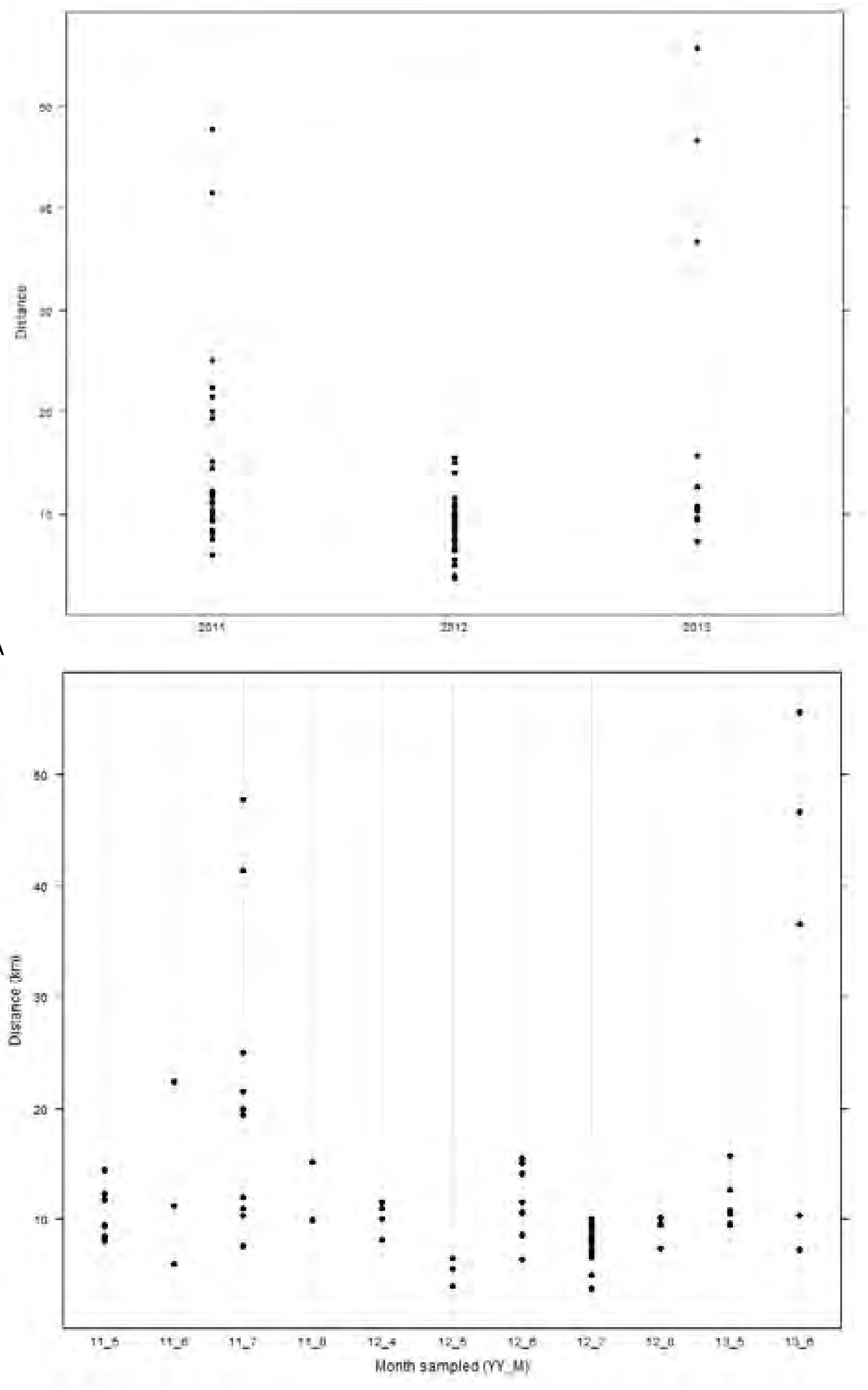


Figure 4.10. Intra- and inter-annual variation of foraging distances (km) travelled from Robben Island by chick-rearing African Penguins (A) yearly variation between 2011 (N = 24), 2012 (N = 35) and 2013 (N = 13) and (B) monthly variation in 2011: May (N = 9), June (N = 3), July (N = 10), August (N = 2); 2012 (N = 4): April (N = 4), May (N = 3), June (N = 8), July (N = 16), August (N = 4), and in 2013 May (N = 7) and June (N = 6).

Dive analysis results

There was evidence that the dive behaviour measures for which there was only one per foraging trip had significant inter-annual differences in mean except for percentage of time diving, dive frequency and CPUE (Table 4.6). Tukey pair-wise comparison tests revealed significant differences between 2012 an 2011 for all measures, and between 2012 and 2013 for the number of dives and foraging dives and between 2011 and 2013 in the number of wiggles and the median DE (Table 4.7).The mixed effects models for the dive behaviour measures for which there were multiple measures per individual showed that there were no significant differences between the sexes (Table 4.8). The mixed effects models also showed that in terms of dive behaviour only bottom phase duration and dive efficiency differed between years (Table 4.8). Plotting the effect sizes of the models indicated bottom phase duration in 2011 was on average 25% longer in duration than of bottom phase durations in 2012 and 42% longer than bottom phase durations in 2013; these higher bottom phases in the dive cycle are likely the reason dive efficiency was ca. 30% greater in 2011 in than in the other years (Fig. 4.11).

Table 4.6. Inter-annual comparison of dive behaviour measures with the mean ± SE (range) of measures presented from 74 African Penguins rearing chicks at Robben Island.

	All years	**Year**			**Parametric test**
Dive behaviour	*N* = 74	**2011** *N* = 26	**2012** *N* = 37	**2013** *N* = 11	**ANOVA results**
No. Dives	351 ± 18 (213–1008)	487 ± 37 (234–1008)	330 ± 15 (213–574)	480 ± 44 (312–890)	$F_{2,71} = 11.32$, $p < 0.001$
No. Foraging dives (> 3m)	285 ± 17 (106–894)	411 ± 32 (216–894)	256 ± 14 (106–497)	405 ± 44 (259–789)	$F_{2,71} = 13.5$, $p < 0.001$
Time diving (h)	5.0 ± 0.3 (1.9–13.9)	7.1 ± 0.6 (3.3–13.5)	4.4 ± 0.2 (1.9–5.9)	6.0 ± 0.8 (4.6–13.9)	$F_{2,71} = 13.5$, $p < 0.001$
Dive frequency (dives h^{-1})	31.5 ± 1.1 (15.1–55.6)	33.5 ± 1.8 (17.0–50.3)	31.2 ± 1.4 (15.1–55.0)	38.4 ± 2.9 (22.9–55.6)	$F_{2,71} = 2.84$, $p = 0.07$
Time diving (%)	44 ± 1 (21–64)	47 ± 2 (28–64)	41 ± 2 (21–64)	46 ± 3 (32–63%)	$F_{2,71} = 3.22$, $p = 0.05$
Vertical distance travelled (km)	11.2 ± 0.6 (2.5–29.8)	14.8 ± 1.2 (6.9–29.8)	9.9 ± 0.5 (2.5–15.3)	12.4 ± 1.5 (6.2–25.9)	$F_{2,71} = 8.06$, $p = 0.001$
No. Wiggles	131 ± 18 (25–752)	266 ± 40 (52–752)	104 ± 10 (25–258)	148 ± 39 (34–422)	$F_{2,71} = 10.89$, $p < 0.001$
Catch per unit effort (CPUE) (Wiggles min^{-1})	1.5 ± 0.1 (0.4–3.7)	1.74 ± 0.2 (0.5–3.6)	1.5 ± 0.1 (0.4–2.9)	1.3 ± 0.2 (0.5–2.4)	$F_{2,71} = 1.87$, $p = 0.16$
Median dive efficiency	0.17 ± 0.008 (0.03 – 0.40)	0.22 ± 0.01 (0.13–0.40)	0.15 ± 0.01 (0.03–0.30)	0.15 ± 0.02 (0.08–0.26)	$F_{2,71} = 12.04$, $p < 0.001$

Table 4.7. Post-hoc Tukey honest significance difference pair comparison results for dive behaviour measures for which there was one per individual (per first trip) for 74 African Penguins. The dive measures investigated were number of dives, number of foraging dives (depths > 3 m), time diving, percent of time diving, vertical distance, number of wiggles, the catch per unit effort (CPUE) and median dive efficiency (DE). Dive efficiency is the proportion of the bottom phase duration to the rest of the dive cycle (Eqn. 4.1). Examining the median DE values for each trip avoids bias from any long post-dive intervals.

Parameter	Year comparison	Mean difference	95% CI	*p*-value
No. Dives	2012-2011	−157	−243 – −71	< 0.001
	2013-2011	−7	−128 – 113	0.99
	2013-2012	150	35 – 265	0.01
No. Foraging Dives	2012-2011	−155	−233 – −77	< 0.001
	2013-2011	−6	−115 – 103	0.99
	2013-2012	149	45 – 253	0.003
Time Diving (h)	2012-2011	−2.74	−4.02 – −1.46	< 0.001
	2013-2011	−1.11	−2.90 – 0.69	0.31
	2013-2012	1.63	-0.08 – 3.35	0.06
Time diving (%)	2012-2011	−6	−13 – 0	0.05
	2013-2011	−1	−10 – 8	0.95
	2013-2012	5	−3 – 14	0.30
Vertical distance (km)	2012-2011	−4.9	−7.8 – −2.0	< 0.001
	2013-2011	−2.4	−6.5 – 1.7	0.34
	2013-2012	2.5	−1.4 – 6.4	0.29
No. Wiggles	2012-2011	−163	−247 – −79	< 0.001
	2013-2011	−118	−236 – 0	0.05
	2013-2012	44	−68 – 157	0.61

Table 4.8. Linear-mixed effects model results for dive behaviour of 70 African Penguins of known sex that were provisioning chicks at Robben Island. The mean ± SD and (range) for dive depth, dive duration, bottom phase duration, post-dive intervals and dive efficiency (DE) were investigated with year and sex as fixed effects and the bird ID as a random effect.

Dive behaviour	**Year**						**Significance**	
	2011		**2012**		**2013**			
	Females	Males	Females	Males	Females	Males		
	N = 16	N = 8	N = 14	N = 22	N = 3	N = 7		
	Dives = 8,138	Dives = 3,980	Dives = 4,719	Dives = 7,220	Dives = 1,299	Dives = 3,523	**Sex**	**Year**
Dive depth (m)	15.7 ± 11.9 (max: 68.4)	12.5 ± 11.2 (max: 48.7)	14.8 ± 12.3 (max: 61.7)	14.8 ± 13.8 (max: 61.7)	13.1 ± 11.2 (max: 43.1)	12.7 ±9.8 (max: 50.9)	ns	ns
Dive duration (s)	53.6 ± 26.3 (2–148)	45.9 ± 26.3 (3–139)	46.3 ± 25.9 (3–132)	47.5 ± 25.9 (3–209)	42.2 ± 24.1 (3–106)	45.1 ± 24.5 (3–122)	ns	ns
Bottom phase duration (s)	17.8 ± 14.3 (0–104)	15.3 ± 13.9 (0–93)	11.3 ± 11.4 (0–68)	13.2 ± 13.4 (0-94)	9.6 ± 10.1 (0–52)	12.9 ± 12.6 (0–70)	ns	$F_{66, 23,188} = 6.8$, $p = 0.002$
Post-dive intervals (s)	95 ± 1,784 (0–127270)	77 ± 1,171 (0–52090)	71 ± 632 (0–34670)	62 ± 720 (0–59510)	41 ± 137 (0–3574)	58 ± 626 (0–34412)	ns	ns
DE	0.21 ± 0.16 (0–1.88)	0.21 ± 0.19 (0–3.92)	0.15 ± 0.14 (0–0.82)	0.17 ± 0.16 (0–0.86)	0.15 ± 0.15 (0–0.89)	0.18 ± 0.16 (0–0.87)	ns	$F_{66, 28,809} = 13.6$, $p < 0.001$

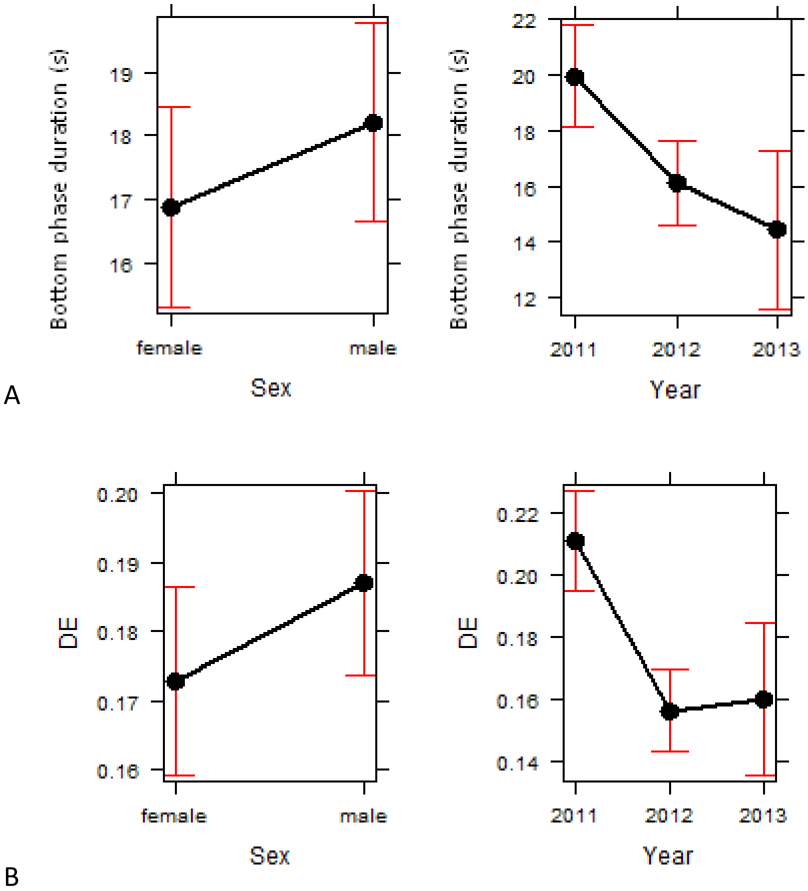


Figure 4.11. Effect sizes plots of sex and year on (A) bottom phase durations and (B) dive efficiency (DE) of dive behaviour of 70 African Penguins raising small chicks at Robben Island. Bird ID was a random effect in the model.

Foraging area results

Inter- and intra-annual spatial variation

The MCPs showed variation in total foraging area between years with 2013 having covered the largest area followed by 2011 and 2012 having the smallest area despite having the greatest number of penguins sampled (Fig. 4.12). The core foraging areas of chick-rearing African Penguins also varied annually (Fig. 4.13). The foraging range area in 2012 was 51.5% smaller than in 2011 and 61.8% smaller than in 2013 (Fig. 4.13). While there was variation in core foraging area size and shape their relative locations in relation to the island remained analogous for all years (Fig. 4.13A). The kernel density estimation of the foraging dives of all years together showed the core foraging area was similar to those on a yearly basis (Fig. 4.14). Overlaying the core foraging area and overall range over the bathymetry depth contours around the island showed core foraging areas are all within areas where the depth is < 50 m deep (Fig. 4.14). The core foraging area and 97% of the foraging range area for all years combined were within a distance of 20 km of the island.

The core foraging areas varied within-years (Fig. 4.15). Sample sizes were not identical for each month and while this may influence results having larger samples did not always increase the foraging area found. For example, in July 2012 there were 16 individuals sampled and the core foraging area was 23.8 km^2 while in June 2012 half that number were sampled (N = 8) and the foraging area covered was larger 36.6 km^2 (Fig. 4.15). Furthermore, in July 2011 there were 10 penguins sampled and the foraging area was 49.9 km^2 (Fig. 4.15). Therefore, it cannot simply be argued that larger samples alone increases core foraging area. In addition, some years showed more within-year variation than others; for example, there was more intra-annual variation in the core foraging areas in 2011 than in 2012 (Fig. 4.15).

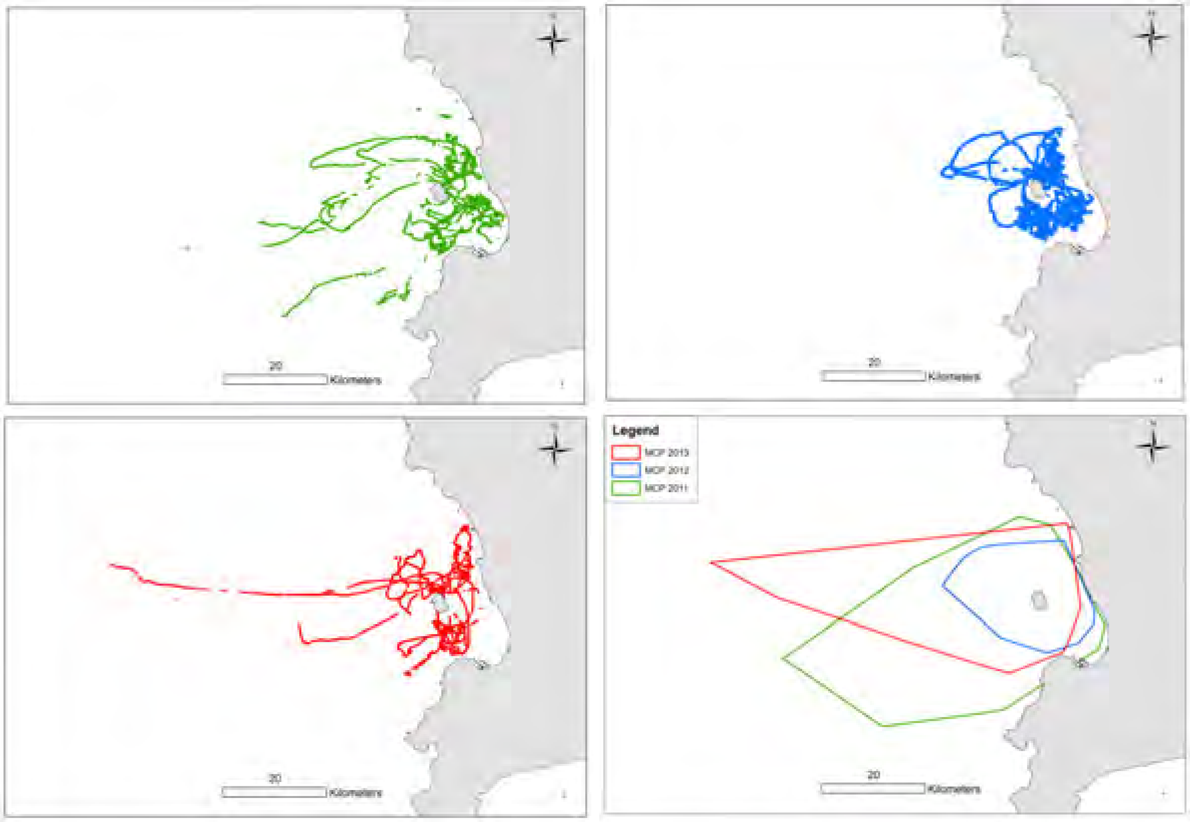


Figure 4.12. Maps of the spatial locations of foraging dives (depth > 3 m) of chick-rearing African Penguins at Robben Island, including the foraging dives from trips that were only partially recorded. Top left shows 6,433 foraging dives in 2011 in green from 27 penguins. Top right shows 6,528 foraging dives in 2012 in blue from 35 penguins. Bottom left shows 4,657 foraging dives in 2013 in red from 13 penguins. Bottom right are the MCPs of all the dives for each year for inter-annual comparisons (2011 in green contains an area of 1,215.9 km^2, 2012 in blue contains an area of 359.6 km^2 and 2013 in red contains an area of 978.1 km^2).

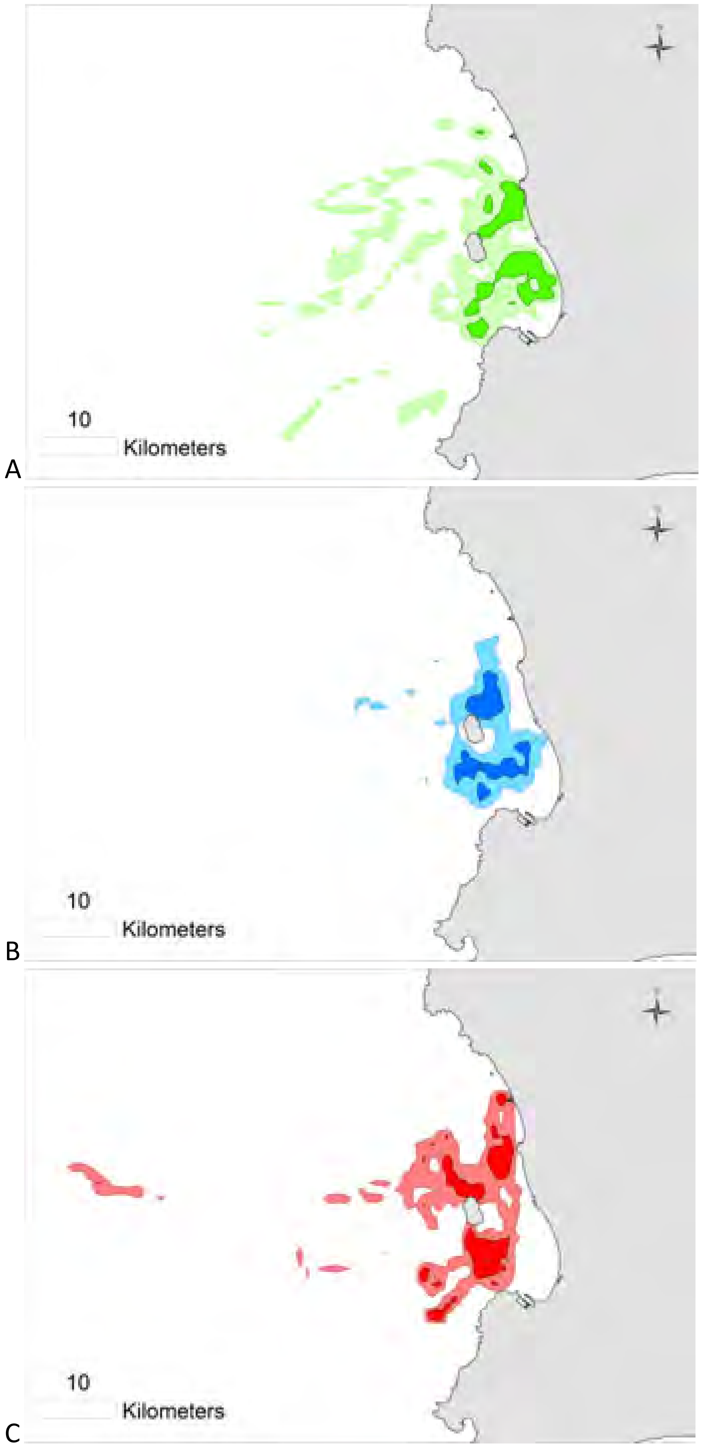


Figure 4.13. Maps of the African Penguin core foraging area (50% volume contour) shown as the darker colour and the home range (90% volume contour) depicted by the lighter colour from the foraging dives of breeding adults provisioning for chicks in (A) 2011 in green from the tracking of 27 penguins, (B) 2012 in blue from the tracking of 35 penguins and (C) 2013 in red from tracking 13 penguins. Core foraging

areas in 2011, 2012 and 2013 were 61.8 km^2, 42.0 km^2, and 56.3 km^2, respectively while foraging home range areas were 275.9 km^2, 142.1 km^2 and 229 km^2.

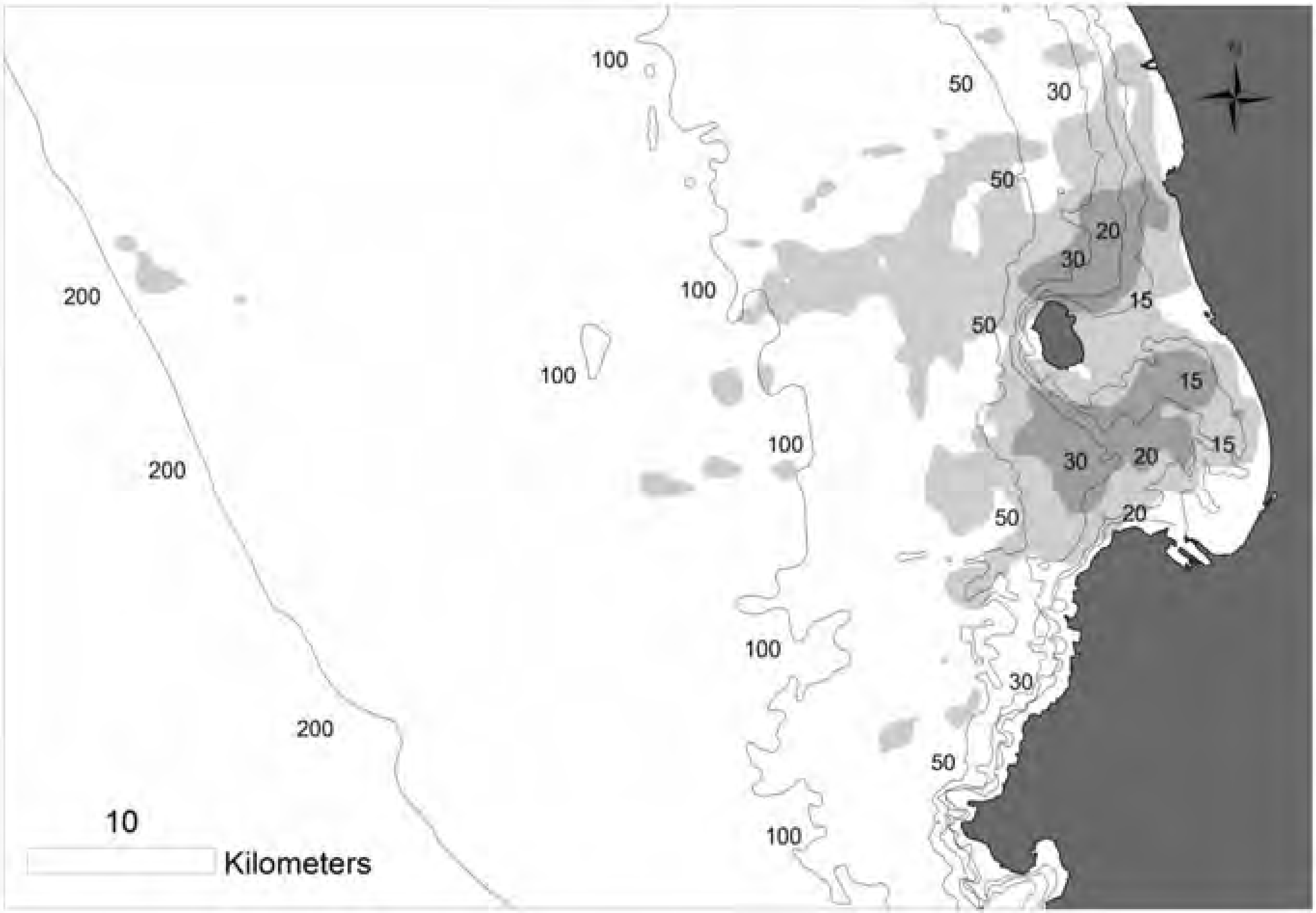


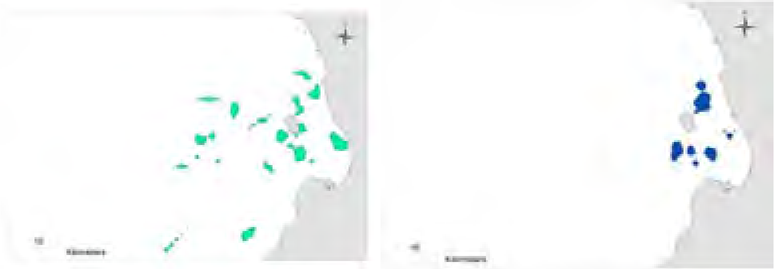
Figure 4.14. Core foraging area (50% volume contour) in medium grey and foraging range area (90% volume contour) in light grey from the foraging dives of 75 African Penguins rearing small chicks at Robben Island and surrounding bathymetry depth contours in meters. Foraging data pooled from all three study years: 2011, 2012 and 2013. The core foraging area for those years combined was 78.3 km^2 and the foraging range area was 347.5 km^2.

2011 **2012** **2013**

April 2012 (N = 4)

May 2011 (N = 12) May 2012 (N = 3) May 2013 (N = 8)

June 2011 (N = 3) June 2012 (N = 8) June 2013 (N = 5)



July 2011 (N = 10) July 2012 (N = 16)

August 2011 (N = 2) August 2011 (N = 4)

Figure 4.15. Monthly core foraging areas (50% volume contour) of the foraging dives of African Penguins rearing small chicks at Robben Island for each month sampled in 2011, 2012 and 2013.

Sex comparison of foraging areas

The median foraging distance from the colony for females was 10 km (range: 3.4–47.7 km, N = 33) and males 9.6 km (range: 5.0–55.6 km, N = 35). Distributions were skewed to the right for both sexes and differences in distribution were not significant (Mann Whitney *U*-test: *W* = 596, p = 0.83). The total MCP of the 68 sexed African Penguins was 1,660.5 km^2. The female MCP area was 1,065 km^2 and smaller than the male MCP area of 1,254.3 km^2; they covered 64% and 76% of the total area, respectively (Fig. 4.16). However, looking at the foraging dives the MCPs appear strongly influenced by a few individuals and visual examination the foraging dives shows considerable overlap between male and female foraging areas (Fig. 4.16).

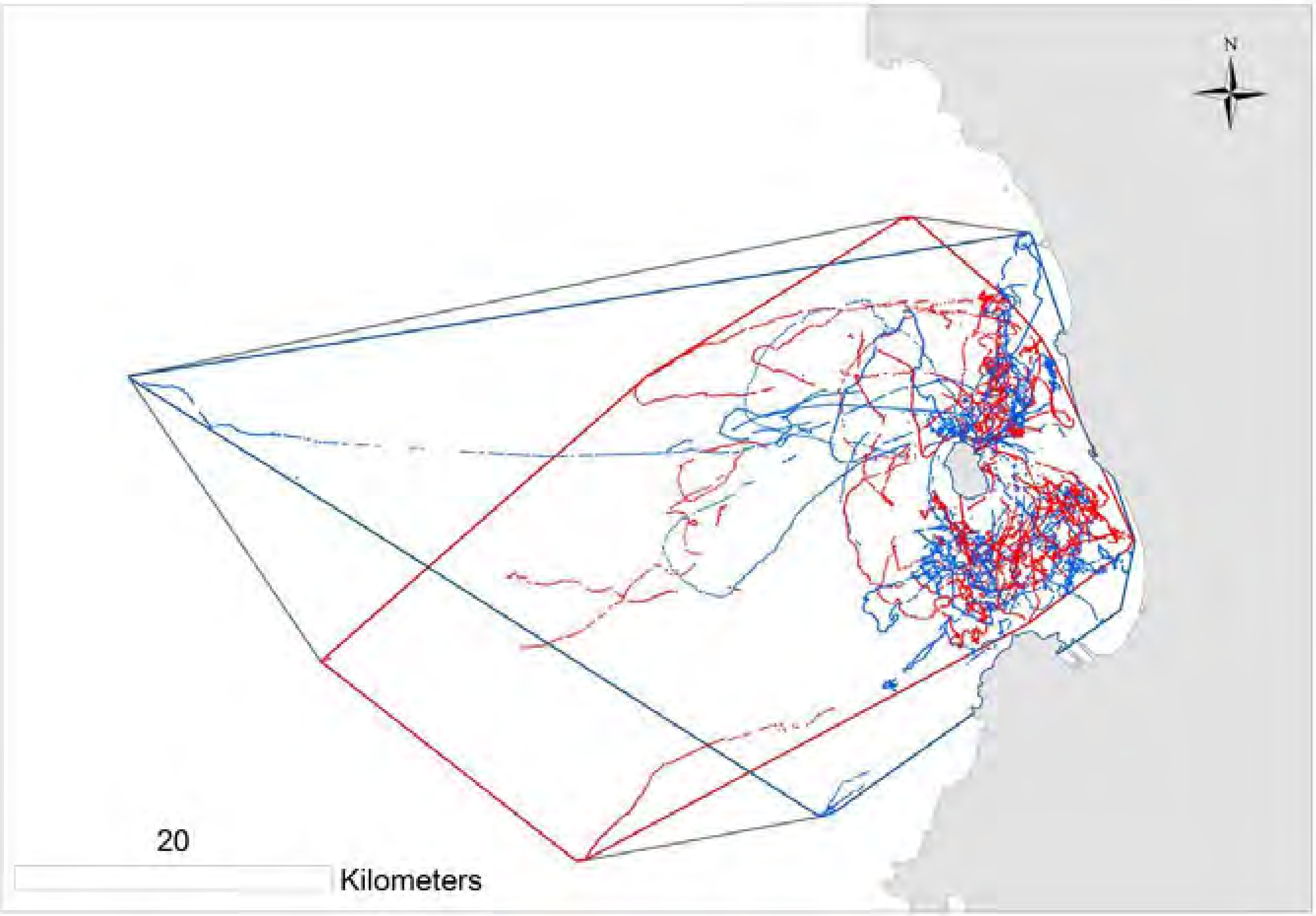
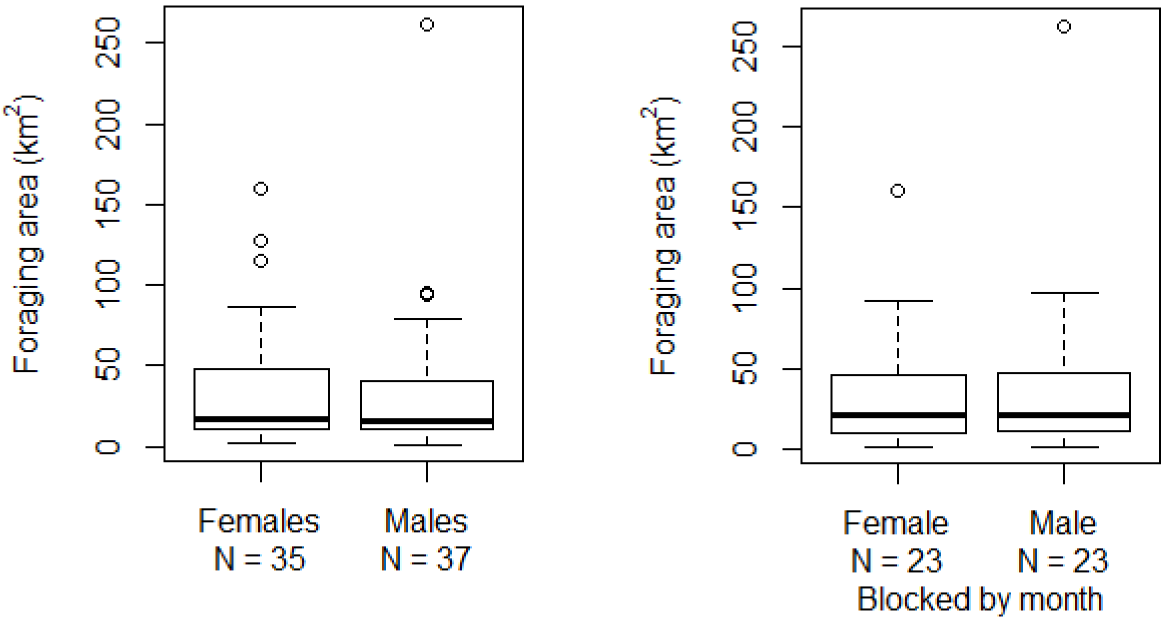


Figure 4.16. Minimum convex polygons (MCP) for all foraging dives from sexed, African Penguins provisioning for chicks. The 100% MCP for all birds shown in gray, the MCP for 33 females shown in red and MCP for 35 males shown in blue. The foraging dives (depth > 3 m) are also shown for the 8,208 male foraging dives in blue and 7,746 female foraging dives shown in red.

MCP foraging areas computed for each individual gave foraging areas for 33 females and 35 males (Fig. 4.17A); the median female foraging area was 16.5 km^2 (range: 1.8–159.7 km^2) and the median male foraging area was 15.4 km^2 (range: 0.7–262.2 km^2). There was no evidence for difference in distribution of foraging area size (Mann Whitney U test: *W* = 596, p = 0.83) (Fig. 4.17A). Blocking by month, and picking the penguins which had been at-sea temporally closest to remove the environmental variability, yielded small but equal sample sizes of 23 for each of the sexes. The foraging areas computed from MCP for each individual showed females had mean (± SE) foraging areas of 33.7 ± 7.6 km^2 (range: 1.8–159.9 km^2) while males were 41.7 ± 11.7 km^2 (range: 1.6–262.2 km^2). The sexes were not significantly different (t_{44} = −0.58, p = 0.57) (Fig. 4.17B).



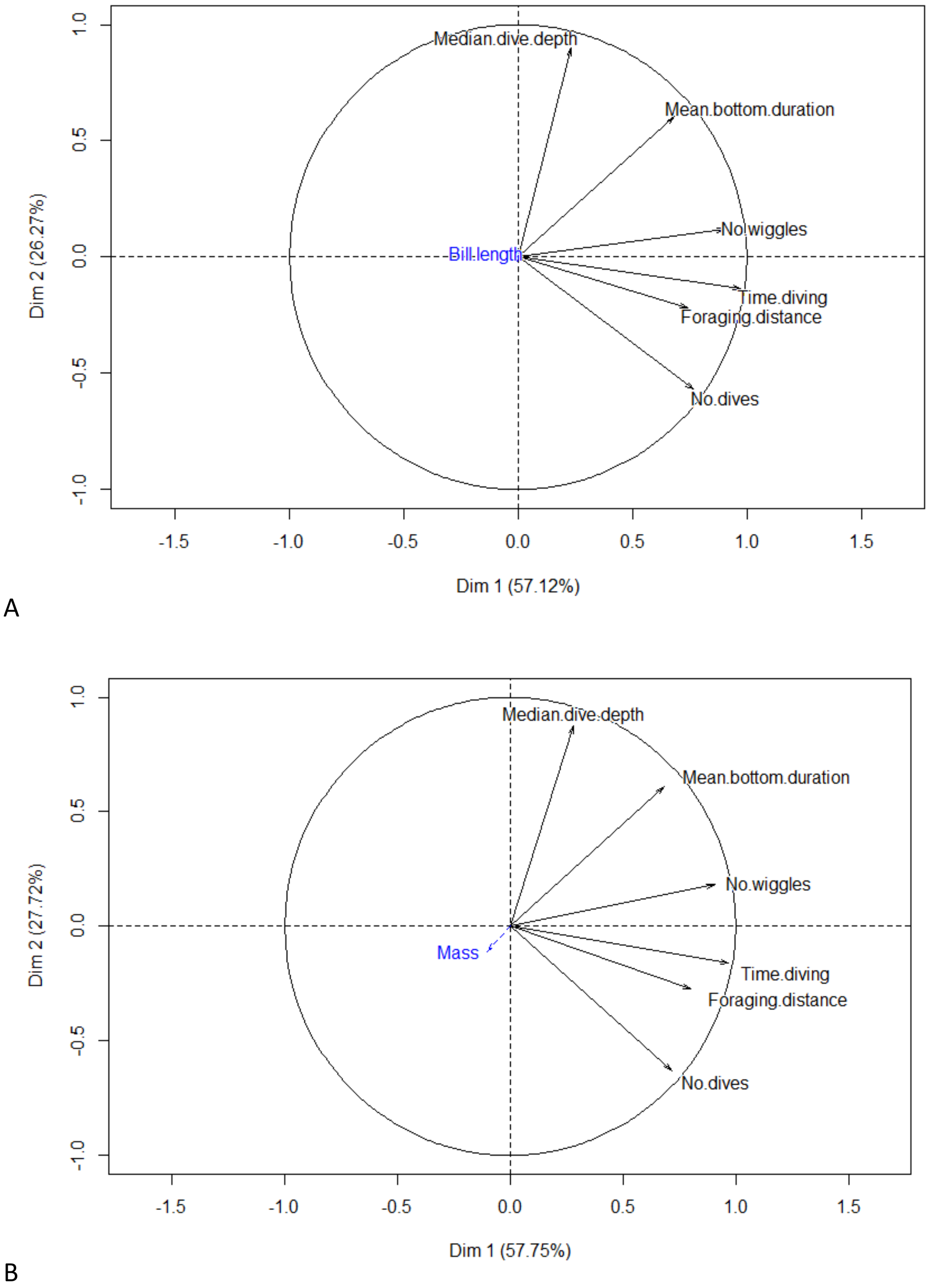
A B

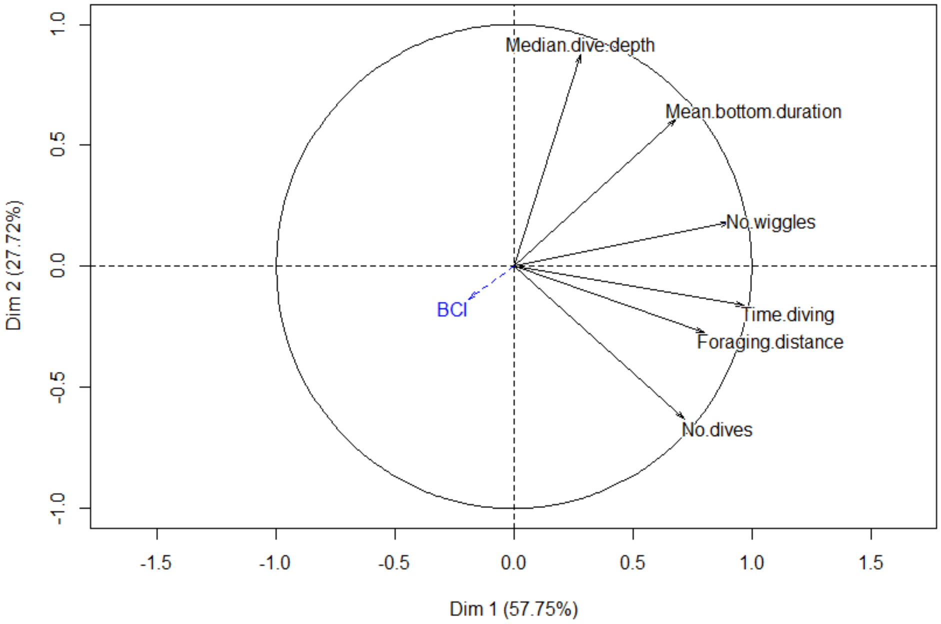
Figure. 4.17. Box and whisker plots comparing the size of the foraging areas of the sexes from individual MCPs of foraging dives for (A) all sexed chick-rearing African Penguins and (B) samples blocked by month. The midline is the median, the box extends to the lower and upper quartiles and the whiskers extend to the extremes within the inter-quartile range and circles show the outliers.

Factors in relation to foraging behaviour

Intrinsic factors: bird structural size, body mass and body condition

The bill length mean (± SE) of the 76 equipped African Penguins with complete data sets was 57.5 ± 0.4 mm (range: 50.8–64.1 mm). No significant differences in the mean were found between years indicating the penguins in the study were of similar structural sizes (ANOVA: $F_{1,72}$ = 2.97, p = 0.09). The body mass of the 73 penguins equipped with devices that had were weighed had mean (± SE) body mass of 2.77 ± 0.04 kg (range: 2.20–3.50 kg). Bird Condition Index (BCI) of equipped birds had a mean (± SE) of 0.33 ± 0.20 BCI (range: −0.12–0.81 BCI). The mean body mass and BCI did not differ significantly between years (Table 4.8). The PCAs indicated the intrinsic factors of body condition and structural size had little to no influence on foraging measures (Fig. 4.18). Furthermore, no subsequent significant correlations were identified between those intrinsic factors and foraging measures.





C

Figure 4.18. Intrinsic variables factor map of the principal component analysis (PCA) of six foraging behaviour measures: median dive depth (m), mean bottom duration (sec), the number of wiggles, time diving (h), foraging distance (km) and the number of dives with a supplementary intrinsic variable of interest shown in blue with dashed arrows: (A) bill length (mm) an indicator of African Penguin size (mm) (N = 68), (B) mass (kg) of African Penguins (N = 66) and (C) body condition index (BCI) of African Penguins(N = 66). Bill length was not related to any of the foraging parameters, nor was mass. BCI had weak negative relationships to the foraging parameters. BCI was independent of the number of dives and weakly negatively correlated to the remaining foraging parameters but none of the correlations were significant (p > 0.05).

Extrinsic factors: brood mass and wave conditions

The brood mass mean (± SE) was 1.38 ± 0.06 kg (range: 0.44–2.92 kg), and the timing of measurements varied on average by two days (range: 0–11 days) after the equipped bird was at-sea. There were 13 samples of brood mass measured at deployment and 10 of those had all the foraging behavioural measures of interest for the PCA analysis. For brood mass measured two days from the day the equipped bird was at-sea there were was a sample of 41 and 37 had the corresponding foraging measures for the PCA analysis. The PCA analysis indicated brood mass at deployment was strongly related to foraging behaviour measures while brood mass two days from the time the equipped bird was at-sea was not related to the foraging behaviour (Fig. 4.19). Both median dive depth and time diving had a strong positive correlations with brood mass at deployment (Fig. 4.19). Linear regressions of these indicated brood mass at deployment explained some of the time the parent spent diving, the adjusted R^2 was 0.24 ($F_{1,10}$ = 4.49, p = 0.06) but the sample size was small and there is a 6% chance it was by chance. The regression of brood mass at deployment explained by median dive depth was not significant ($R^2 = 0.16$, $F_{1,10} = 2.34$, p= 0.16) but indicated that if a relationship exists it is a weak one.

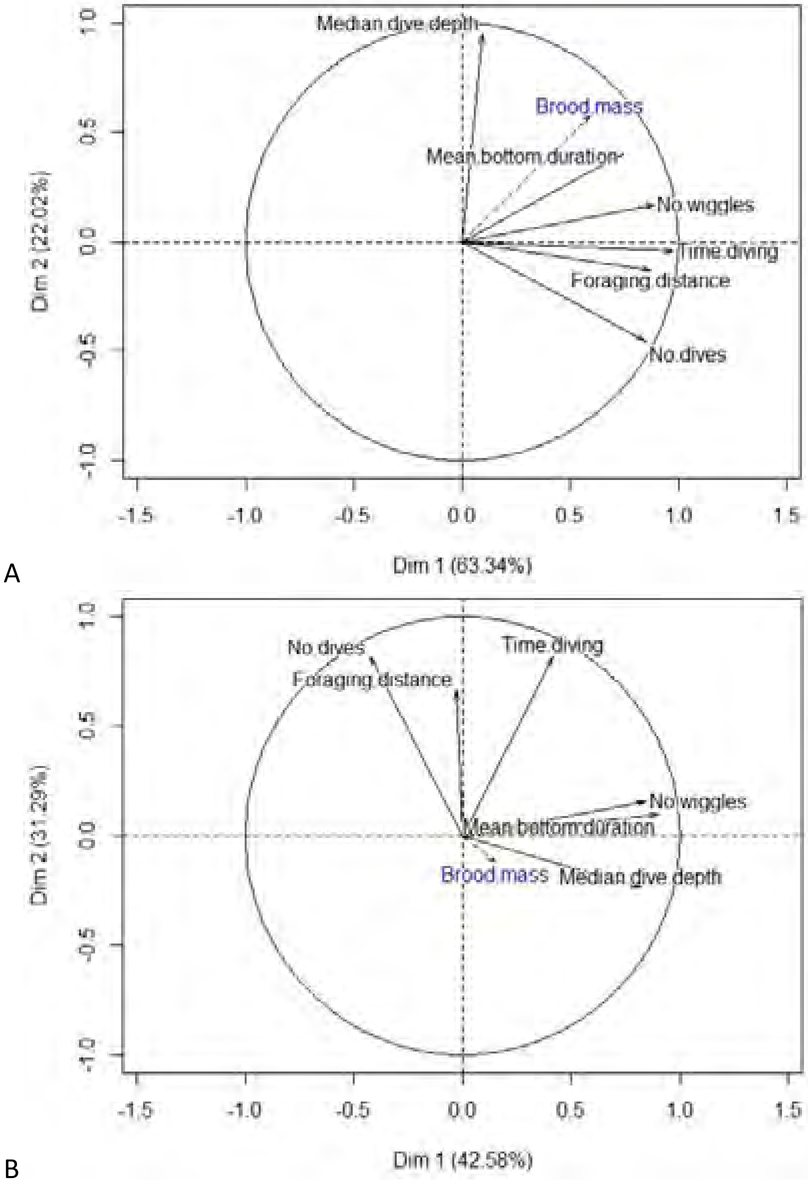


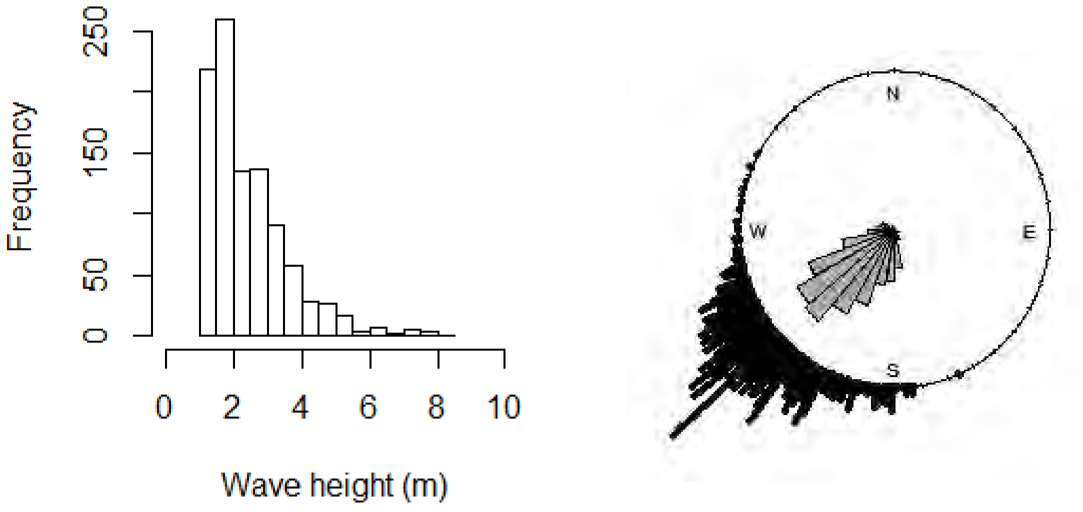
Figure 4.19. Brood mass variables factor map of the principal component analysis (PCA) of brood mass in relation to six foraging behaviour measures: median dive depth (m), mean bottom duration (s), the number of wiggles, number of dives, time diving (h), foraging distance (km). The supplementary variables of interest shown with blue factor arrows with dashed lines: (A) Brood mass (kg) at deployment (N = 10) (B) Brood mass (kg) at two days following the date the equipped bird was at sea (N = 37). Brood mass at deployment was strongly related to the foraging measures. Brood mass at deployment had a strong positive correlation to median dive depth (r = 0.75, $t_8 = 0.01$, p = 0.013) and evidence of a strong positive relationship with time diving (r = 0.63, $t_8 = 2.27$, p = 0.050). The other measures were positively correlated but not significantly (p > 0.05). Brood mass measured two days from the day the equipped bird was at sea was weakly related to foraging behaviour measures, none of the correlations were significant.

In terms of annual comparisons of brood mass, there were no significant differences in the means between years in brood mass when measured within two days of the equipped bird's at-sea trip (Table 4.9). While I was not able to check for a difference in brood mass at deployment between years, considering sampling was conducted the same way and restricted to small sized chicks it is unlikely there were substantial differences in brood mass between years at deployment time.

Table 4.9. Inter-annual comparisons of intrinsic factors, body mass and condition, of African Penguins equipped with logger devices and extrinsic factors which were the wave conditions while equipped penguins were at-sea and the brood mass measured within two days of the date the equipped bird was at-sea.

	Year Mean ±SE (range) *N*			
Variable	2011	2012	2013	ANOVA
Body mass (kg)	2.66 ± 0.06 (2.27–3.5) *25*	2.83 ± 0.05 (2.2–3.38) *37*	2.79 ± 0.09 (2.26–3.16) *11*	$F_{2,70} = 2.55$, p = 0.09
Body condition index	0.26 ± 0.03 (0.33–0.78) *25*	0.36 ± 0.03 (-0.1–0.81) *37*	0.30 ± 0.09 (-0.01–0.69) *11*	$F_{2,70} = 2.15$, p = 0.13
Mean wave height (m)	2.51 ± 0.28 (1.11–6.74) *27*	2.75 ± 0.16 (1.67–4.88) *35*	1.91 ± 0.16 (1.26–2.87) *11*	$F_{2,70} = 2.33$, p = 0.11
Mean wave direction (°)	225 ± 3 (193–274) *27*	228 ± 3 (185–255) *35*	222 ± 4 (207–244) *11*	$F_{2,70} = 0.74$, p = 0.48
Brood mass (kg)	1.24 ± 0.14 (0.44–2.53) *15*	1.35 ± 0.08 (0.50–2.25) *32*	1.56 ± 0.24 (0.46–2.92) *9*	$F_{2,53} = 0.98$, p = 0.38

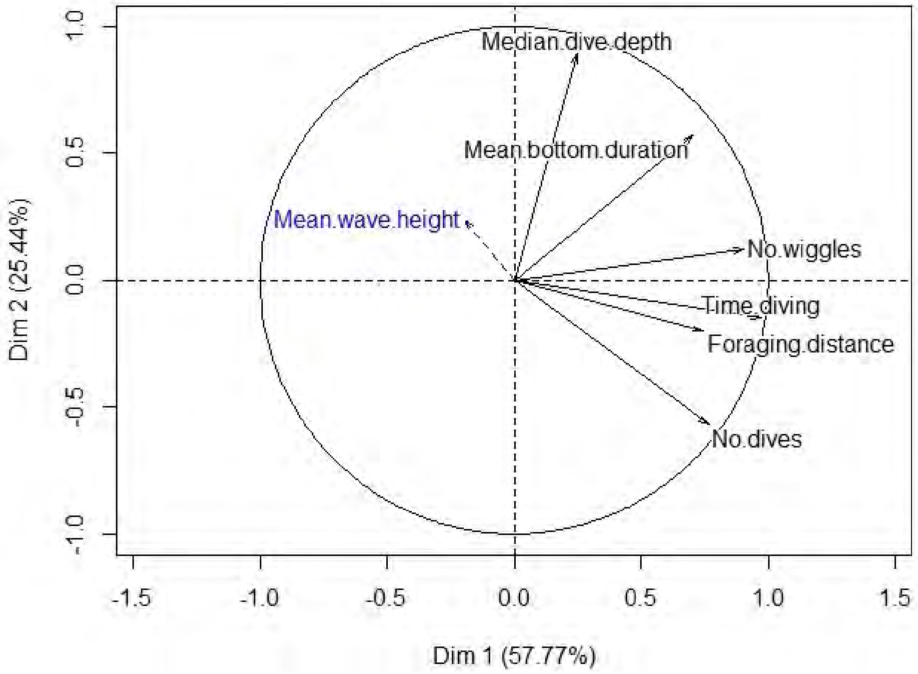
As for the sea conditions, for the 996 unique hours African Penguins were at-sea with devices, wave condition data were available for 993 of those (99.7%). Wave height was skewed to the right with the median wave height being 2.1 m (range: 1.11–6.74 m) for the hours penguins were at-sea with devices on first trips (Fig. 4.20A). Wave direction was normally distributed and predominantly south-westerly; the mean direction (± SD) was 225 ± 20° while the range was from 155° (south-south-east) to 297° (west-north-west) during the hours penguins were at-sea on first trips (Fig. 4.20B). In terms of the hours when penguins were at-sea with devices, there were no significant differences in wave conditions between years (Table 4.9). Wave conditions had weak relations to foraging behaviour measures (Fig. 4.21): foraging distance had a weak negative correlation to mean wave height and direction; the number of dives had a weak negative correlation with mean wave height (Fig. 4.21). Linear regressions of those revealed that mean wave height did not explain the variation in the number of dives (adjusted $R^2 = 0.08$, $F_{1,69} = 7.47$, $p = 0.008$) or the foraging distance (adjusted $R^2 = 0.08$, $F_{1,66} = 6.51$, $p = 0.013$) of breeding penguins. Neither did mean wave direction explain the variation in foraging distance (adjusted $R^2 = 0.05$, $F_{1,66} = 4.86$, $p = 0.013$).



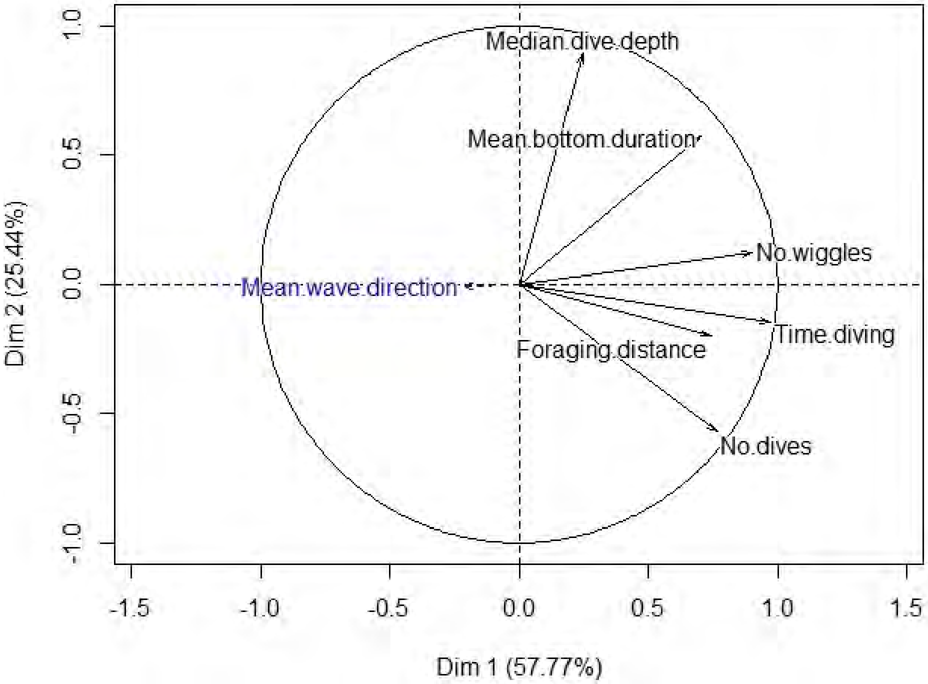
A

B

Figure 4.20. Wave conditions when African Penguins were at sea with devices (N = 993 hours) (A) frequency distribution of wave height and (B) a circular histogram of wave direction points represent 1° and stacked to show frequency of occurance. Rose diagram shown in the middle with 36 bins of 10° show the predominant south westerly direction of waves.



A



B

Figure 4.21. Wave condition variables factor map of the principal component analysis (PCA) of wave conditions in relation to six foraging behaviour measures: median dive depth (m), mean bottom duration (s), the number of wiggles, time diving (h), foraging distance (km) and the number of dives with a for 66 African Penguins. The supplementary variables of interest shown with blue factor arrows with dashed lines of: (A) mean wave height (m) (B) mean wave direction during foraging trip time at sea. The wave conditions were weakly related to foraging behaviour measures. Mean wave height had a weak negative correlation to the number of dives (r = −0.34, t_{64} = −2.90, p = 0.005) and foraging distance (r = −0.31, t_{64} = −2.60, p = 0.010). Mean wave direction was negatively correlated to the foraging distance (r = −0.26, t_{64} = −2.16, p = 0.040). All other correlations were not significant (p > 0.05).

Discussion

This chapter presented foraging behaviour collected with GPS and temperature depth devices from chick-rearing African Penguins throughout several months of the breeding season. The study took place when there was a purse-seine closure out to 20 km around the island and confirmed that African Penguins provisioning chicks consistently made use of this area over the breeding season and in all years investigated; the core foraging area identified from all years combined was within this area (Fig. 4.14).

Kernel density estimations showed foraging areas varied spatially on a yearly basis, and while core foraging areas changed in area they tended to be in analogous locations in relation to Robben Island, north to north-east and south to south-east of the island (Fig. 4.13). The 11 tracks collected in 2003 at Robben Island also show use of those areas (Petersen et al. 2006), providing further evidence of the importance of these areas to provisioning penguins at the Robben Island colony.

In terms of inter-annual differences in behaviour, there were significant differences for GPS track and dive measures (Table 4.4, Table 4.6). However, some measures such as dive durations, dive depths, post-dive intervals, dive frequency and CPUE were comparable for all three years of the study (Table 4.6, Table 4.8). The GPS track measures were comparable between 2011 and 2013 (Table 4.4, Table 4.5). In 2012, chick-rearing African Penguins travelled shorter foraging distances, trip durations were shorter and made less dives and foraging dives per trip than in the two other years of the study (Table 4.4, Table 4.5., Table 4.6, Table 4.7). There were greater numbers of wiggles per trip in 2011 than there were in 2012 and 2013. Furthermore, bottom phase duration was longer and DE was higher in 2011 than in the other two study years (Table 4.6, Table 4.7, Fig. 4.11). Yet, the CPUE did not differ significantly between years. Adult body mass, body condition, brood mass and wave conditions were comparable over the years of the study (Table 4.9) and could not explain the yearly differences found in foraging behaviour. Understanding these differences requires the context of prey availability. The behavioural differences observed need to considered within the context of prey abundance and diet which will be investigated in the next chapter.

African Penguin foraging behaviour was weakly related to wave conditions (Fig. 4.21). Greater foraging distances were related to lower wave heights. It is possible the effect of sea conditions on the foraging behaviour of African Penguin is similar to that on Southern Rockhopper Penguins (*Eudyptes chrysocome*), for which foraging body mass gain is lowest under high mean daily wind speeds and increased with westerly winds which are linked to upwelling (Dehnhard et al. 2013). Waves during storm conditions may hinder the foraging ability of penguins (Dehnhard et al. 2013). Upwelling does not occur during the African Penguin breeding season at Robben Island, but it is possible that other oceanographic features provide foraging cues to prey availability. One such oceanographic feature that penguins use as foraging cues is thermoclines (van Eeden 2012, Pelletier et al. 2012). That foraging distances were greater when wave directions were more southerly than westerly could be linked to oceanographic features but would require further investigation. Overall, the weak relation of a top predator to wave conditions is not surprising considering seabird species' richness and abundance in the Benguela are only weakly explained by physical weather features like wind or sea-state (Abrams and Griffiths 1981). This suggests that seabird distributions are mainly driven by prey type and availability within the limitations of movement from breeding regimes (Abrams and Griffiths 1981).

The kernel density analyses conducted indicate that core foraging areas and ranges varied within-years (Fig. 4.15). In two years of the study, the within-year variation in foraging distances was larger than the between year variation and this warrants further investigation with more years of data. Kernel density analysis accuracy can depend on the bandwidth, the smoothing parameter, used (Seaman and Powell 1996). Kernel density techniques are known to be sensitive to sample sizes (Börger et al. 2006, Robertson et al. 2014). The sample sizes were not equal in this study between years or months because I chose to include all available foraging data. While this is a potential source of error, it is worth noting that larger sample sizes of birds did not necessarily result in larger core foraging areas (Fig. 4.13). The bandwidth and kernel type were chosen for comparability to a gridded approach. Other analytic approaches such as first passage time would likely give similar results (Tancell et al. 2013).

It remains to be seen if dive behaviour is dependent on bathymetry. Hydrodynamic modelling and identification of oceanographic features of seabird marine environments are recommended (Tremblay et al. 2009). Further investigation of the features of the water masses around Robben Island could provide further details of the predator-prey dynamics in the area.

Intrinsic factors showed little to no relation to African Penguin foraging behaviour. African Penguin body condition index (body mass independent of size) was not related to foraging measures is as predicted. This was consistent with findings for Little Penguins (*Eudyptula minor*) and Magellanic Penguins that body mass is not influential on dive behaviour (Walker and Boersma 2003, Zimmer et al. 2010a). African Penguin size as indicated from bill length measurements was not related to foraging behaviour. This was in contrast with diving studies of Magellanic Penguin (Walker and Boersma 2003). In that case, Magellanic Penguin body size was obtained from a principal component analysis of multiple measurements bill length, bill depth, flipper length and foot length. Unfortunately, those body parts were not measured in our study. Penguins use flippers to propel their dives (Elliott et al. 2013), so differences in flipper size would be more likely to influence dive behaviour than bill length. Further analysis could be conducted following Walker and Boersma (2003) if more measurements are taken of penguins equipped with devices. It is also possible that the variation in size of African Penguins sampled was not large enough to determine differences in diving behaviour at Robben Island.

Contrary to expectations, sex-specific effects were not identified in Robben Island foraging behaviour. These findings are contrary to those of African Penguin diving behaviour in Algoa Bay, where Pichegru et al. (2013) found differences in dive depth, duration and rate between the sexes. Furthermore, analysing spatial use in the same way as Pichegru et al. (2013) gave results contrary to the prediction that females were foraging over larger areas than males (Fig. 4.16). The subsequent analysis with individual MCPs was more robust to outliers, showing the foraging areas of the sexes at Robben Island have been comparable (Fig. 4.17). Investigating foraging area with individual MCPs provides a more rigorous approach to investigating sex-specific foraging area differences. Re-examining the sex-specific differences found in the Eastern Cape with this method is recommended.

There are a few potential explanations for sex-specific foraging occurring at Eastern Cape colonies but not at Western Cape colonies. The average and maximum dive depths for birds at Eastern Cape are deeper than those observed for birds in the Western Cape (Table 4.8, Ryan et al. 2007, Pichegru et al. 2012, 2013). Dive depth is correlated with dive duration (Ryan et al. 2007). It is possible that at deeper dive depths the size difference between males and females becomes influential. Deeper diving depths are most likely to be due to a difference in bathymetry. Examining bathymetry maps around St. Croix and Bird Island indicate the depth increases more rapidly there than around Robben Island. Prey could be located deeper in the water column at colonies in the Eastern Cape. It is also plausible that there could be geographic variation in immunocompetence at different colonies as seen in Chinstrap Penguins (*P. antarctica*) (Barbosa et al. 2013). Variation in immunocompetence could impact geographic reproductive investment as has been observed in Tree Swallows (*Tachycineta bicolor*) (Ardia 2005). Even though penguins and swallows are widely separated taxonomically, geographic variation in immunocompetence could occur in penguins. Immunocompetence has been shown to vary between the sexes in Magellanic Penguins (Moreno et al. 2001). Immunocompetence requires further investigation in the African Penguins.

A factor that has not been accounted for in this study of African Penguin foraging behaviour and others to date is age. It is possible that the ages or breeding experience were not sampled equally. Experimental manipulations of European Shags (*Phalacrocorax aristotelis*) show that foraging performance increases with experience (Daunt et al. 2007). There could be behavioural age and sex interactions. In the King Penguin there is evidence of this in trip length, dive behaviour and diet but comparable use of foraging sites (Le Vaillant et al. 2013). A few seabird studies have shown age-specific foraging area differences (e.g. Lecomte et al. 2010, Pelletier et al. 2014). In the Little Penguin dive efficiency is highest in middle age category indicating they are more efficient foragers than penguins in the younger and older age categories (Zimmer et al. 2011) and older penguins use more near-shore foraging areas (Pelletier et al. 2014). Further investigation into the influence of age and breeding experience on provisioning behaviour and foraging area use is recommended in the *Spheniscus* genus.

African Penguin foraging effort is known to be influenced by chick age (Wilson et al. 1989, Wilson and Wilson 1990, Zimmer et al. 2010a) as older chicks have greater energetic demands than younger chicks (Bouwhuis et al. 2007). Penguins foraging for larger chicks need to catch more food (Cooper 1977, Wilson 1985b, Wilson and Wilson 1990). The cumulative mass of chicks per nest has significant effects on foraging trip distance, duration and path length (Pichegru et al. 2013). This explains the finding that brood mass at deployment had strong positive correlation with the time the provisioning penguin spent diving (Fig. 4.19). The findings indicated brood mass at deployment explained almost a quarter of the variation in the time penguins spent diving but sample sizes were small and the results were inconclusive. Brood mass measured at later dates did not relate to foraging behaviours indicating the importance of collecting this measure at deployment.

Device attachment has costs to the study individuals particularly if devices are not well positioned or not streamlined (Wilson et al. 1986, Bannasch et al. 1994, Culik et al. 1994). The possibilities of modified behaviour and possible changes in swimming speeds due to device drag need to be considered (Wilson et al. 1986). There is the risk that equipped penguins behave abnormally or abandon their nests (Wilson 1997, Taylor et al. 2001). However, African Penguins equipped with GPS-TDlog devices during provisioning trips for small chicks have the same trip durations as control birds without devices (Ryan et al. 2004, Petersen et al. 2006, Pichegru et al. 2010). It is possible that penguins equipped with Fastloc 2 and TDRs behaved differently than those equipped with GPS-TDlogs but sample sizes were too small to evaluate this. Comparisons of diving behaviour of Southern Rockhopper Penguins equipped with GPS-TDlog and TDR devices indicate a difference in diving efficiency but not for other dive parameters (Ludynia et al. 2012a). While a difference in behaviour due to device size and shape is likely, considering comparisons of diving behaviour of different *Spheniscus* species were similar even though devices were not the identical (Ryan et al. 2007) indicates that while differences likely exist they are unlikely to be substantially large.

Conclusions

Core foraging area of African Penguins provisioning chicks varied within and between years, yet always included area within 20 km of the island. Foraging areas of the sexes were comparable. Foraging behaviour differed within and between the years investigated, with 2011 and 2013 generally being more similar than in 2012. African Penguins that were provisioning chicks in 2012 travelled shorter foraging distances, trip durations were shorter and made fewer dives per trip than in the two other years of the study. Intrinsic factors (penguin structural size, body mass and body condition) showed little to no correlation to foraging behaviours. Brood mass at deployment was strongly correlated to time diving and median dive depth. Wave conditions provided weak negative correlations to foraging distance and the number of dives but were unable to explain the variation in those behaviours. Neither the intrinsic factors nor the extrinsic factors of brood mass or wave conditions at-sea were able to explain the annual differences in foraging behaviour observed. The next chapter examines whether they can be explained by the context of prey availability around the island.

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Chapter 5

Fine-scale investigation into foraging behaviour of African Penguins provisioning chicks in relation to local prey availability around Robben Island

African Penguin (*Spheniscus demersus*) tracking was conducted at the same time as hydro-acoustic surveys at fine-scales around the colony. In total, 14 penguins were tracked within 2 days of a pelagic fish survey out to a radius of 20 km around the island. PCA variable factor maps were plotted to assist in identification of relationships between estimated fish abundance and African Penguin foraging behaviour measures. It indicated that estimated pelagic fish abundance around the island showed strong negative relations to foraging behaviours. The time penguins spent diving had the strongest negative relationship to prey abundance. Linear regressions indicated local prey abundance explained more than half of the variation in time diving as well as some of the variation in the numbers of wiggles and foraging distance travelled. Prey availability provided an explanation for the annual differences observed in foraging behaviour.

Introduction

The integration of biologging in conjunction with hydro-acoustic surveys provides a new way to investigate seabird behaviour in relation to prey abundance. In foraging ecology, seabirds have been proposed as indicators of prey availability (Cairns 1988, Montevecchi 1993, Furness and Camphuysen 1997, Piatt et al. 2007) and studies have provided evidence of relationships between seabird behaviour and prey abundance (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Kitaysky et al. 2000, Davoren et al. 2003, Grémillet et al. 2004, Burke and Montevecchi 2009, Montevecchi et al. 2012). In these types of investigations, one of the main concerns is whether the predator and prey distributions match at the scale of investigations (Rose and Leggett 1990). Fisheries records (Thomas and Schülein 1988) and seabird counts during transects (Wilson et al. 1988, Davoren et al. 2003, Kokubun et al. 2008) have been used to investigate the relationships between pelagic prey and seabird distributions. The advantage of hydro-acoustic surveys is they provide direct measures of relative fish abundance and distributions (Hampton 1987, Coetzee et al. 2008) as opposed to using catch data as an estimate of prey availability. The miniaturisation of biologging devices has made it possible to compare seabird GPS tracks and pelagic fish hydro-acoustic surveys at multiple scales (Grémillet et al. 2008, Montevecchi et al. 2012, Tew Kai et al. 2013), but as far as I am aware, fine-scale hydro-acoustic fish surveys at in combination with GPS penguin tracking is novel. The fine-scale hydro-acoustic fish surveys sampled pelagic fish density around Robben Island out to a radius of 20 km.

Just as information can be gained from examining seabird-fisheries interactions at fine-scales at (Granadeiro et al. 2011, Torres et al. 2011, 2013, Tew Kai et al. 2013), investigating seabird foraging behaviour at fine-scales provides insight to foraging strategies (e.g. Ropert-Coudert et al. 2004, 2006, Hamer et al. 2009, Watanabe et al. 2014). Fine-scale sampling can also clarify behavioral links to prey abundance and marine predator performance (Boyd 1996). The fine-scale spatial distributions and aggregations of prey are critical to the comprehension of how top marine predators forage (Benoit-Bird et al. 2013). Furthermore, an understanding of the spatial interactions and dynamics at each trophic level (Grémillet et al. 2008) and for different seabird species (Sabarros et al. 2012) are necessary for ecosystem-based fisheries management.

In comparison to other seabirds in the Benguela, African Penguins have constraints that make them vulnerable to ecosystem change: their breeding foraging ranges are more restricted than seabirds which fly (Pichegru et al. 2009) and they do not feed on fisheries waste unlike Cape Gannets (*Morus capensis*) which use it to supplement their diet when pelagic fish availability is low (Tew Kai et al. 2013, Crawford et al. 2014). Studies of African Penguin and prey interactions have been investigated with transects and boat observations (Wilson et al. 1988, Ryan et al. 2012). The foraging areas of breeding African Penguins are known to overlap with pelagic fisheries (Pichegru et al. 2009). In the case of the African Penguin, it has been assumed that increased foraging effort indicates low food availability (Petersen et al. 2006). This chapter will investigate this with the simultaneous GPS tracking of African Penguins and fine-scale fish surveys in the feeding zone around a penguin colony. It seeks to answer the question of whether chick-rearing African Penguin foraging effort is associated with local prey abundance.

Anchovy dominates the diet of breeding African Penguins at Western Cape colonies such as Robben Island (Crawford et al. 2011, Sherley et al. 2013). Anchovy make vertical diel migrations i.e. dispersing at the surface at night to feed on zooplankton and returning to dense shoals at midwater and demersal layers during the day (James 1987). Although their prey are closer to the surface at night, African Penguins seldom feed then indicating light is required for effective prey detection and capture; there is a selection pressure for prey to be at deeper depth or varied depths to avoid predation during the day (Wilson et al. 1993). Anchovy and Sardine shoal together in the southern Benguela during their younger life-history stages when they aggregate inshore along the west coast from March to August (van der Lingen et al. 2006). Recruits pass by Robben Island on the southward migration from nursery to spawning areas (Crawford 1980, Crawford et al. 2006).

A 20 km purse seine fishing moratorium was in place around Robben Island from the period of 2011 to 2013 as part of a government-led feasibility study investigating the impacts of fisheries closure zones around African Penguin island colonies. Fine-scale hydro-acoustic surveys took place around the island. This resulted in a unique opportunity to examine the dynamics of seabird foraging behaviour in relation to the relative abundance and distribution of pelagic fish around an African Penguin colony. The aims of this chapter are to: (1) identify fish densities at which chick-rearing African Penguins forage at around Robben Island, (2) compare the penguin foraging behaviour between times of relatively high and low pelagic fish abundance around the island, and (3) address whether prey abundance is related to the foraging behaviour of chick-rearing African Penguins.

Methods

Ethics

The African Penguin research was conducted under the auspices of the South African Government's Ocean and Coasts branch of the Department of Environmental Affairs (DEA). The penguin handling, techniques and monitoring were approved by DEA, the Robben Island Museum and the University of Cape Town Science Faculty Animal Research Ethics Committee. It was conducted as part of an Island Closures Task Team study for the Small Pelagic Scientific Working Group at the Department of Agriculture Forestry and Fisheries (DAFF).

Data collection

Data collection took place in 2011, 2012 and 2013 at Robben Island (Table Bay, 33°48’S, 18°22’E), a west coast island colony in South Africa (Fig. 3.1). During these years there was a 20 km purse-seine fishing closure in place around the island (Coetzee 2014).

Pelagic fish hydro-acoustic surveys

DAFF conducted the fine-scale hydro-acoustic surveys within a 20 km radius around the island from an inflatable boat "Echo" with a standard SIMRAD 38 kHz echo-sounder system comprising a pole-mounted transducer suspended over the side of the boat and a splash proof console-housed GPS (Merkle et al. 2012a, 2012b). The surveys were transects that curved laterally around the island (Fig. 5.1). Surveys were highly weather-dependant and took two days to complete. Typically, they started at the north end of the island and went southwards except on June 2011 when the survey was reversed (started from the south end for logistical reasons). Multiple fine-scale surveys were conducted during the year. Annual large-scale hydro-acoustic surveys of pelagic fish recruitment over the South African coast line over a distance > 1,400 km were conducted in May–June by DAFF; they provide a background of the large-scale conditions of prey recruitment (Fig. 5.2). Anchovy recruits were less than 10 cm and Sardine recruits less than 12 cm (Mhlongo et al. 2012, Phillips et al. 2013). The fine-scale hydro-acoustic surveys covered an area of <400 km^2 while the large-scale surveys covered a an area > 150,000 km^2.

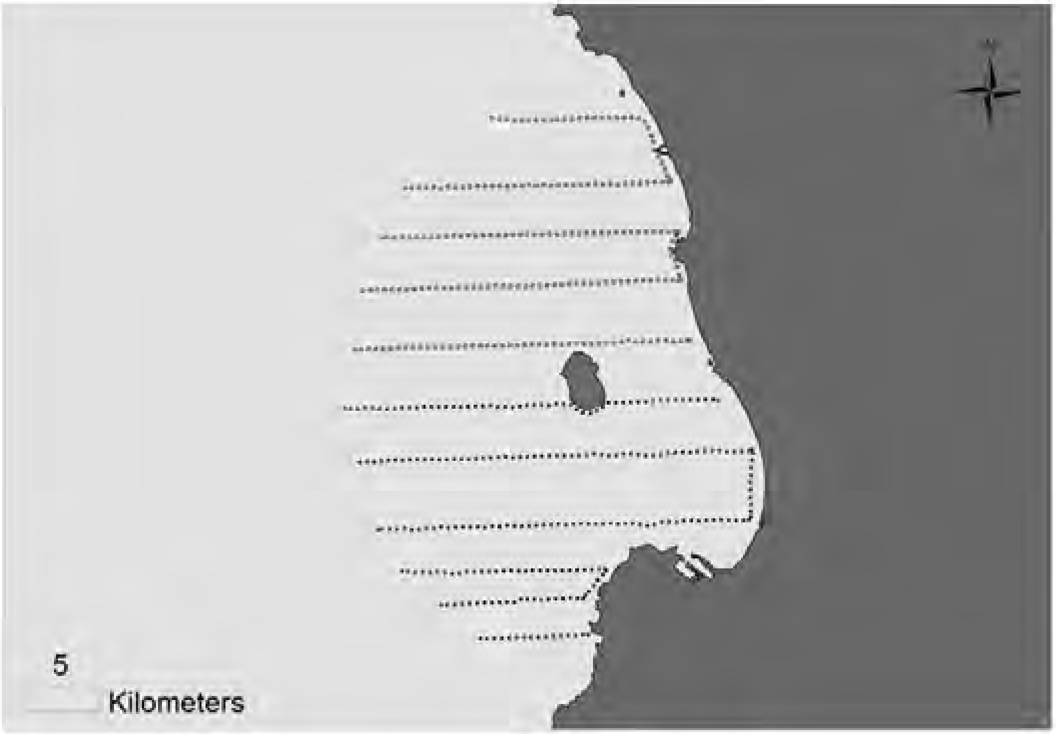


Figure 5.1. The fine-scale hydro-acoustic survey transects around Robben Island. Typically conducted from north two south with the section in grey points showing the sampling points covered on the first day and black points the sampling points covered the second day. The transect lines were less than 5 km apart. The survey points along the transect were c. 450 m apart. Each survey was comprised of c. 500 survey points.

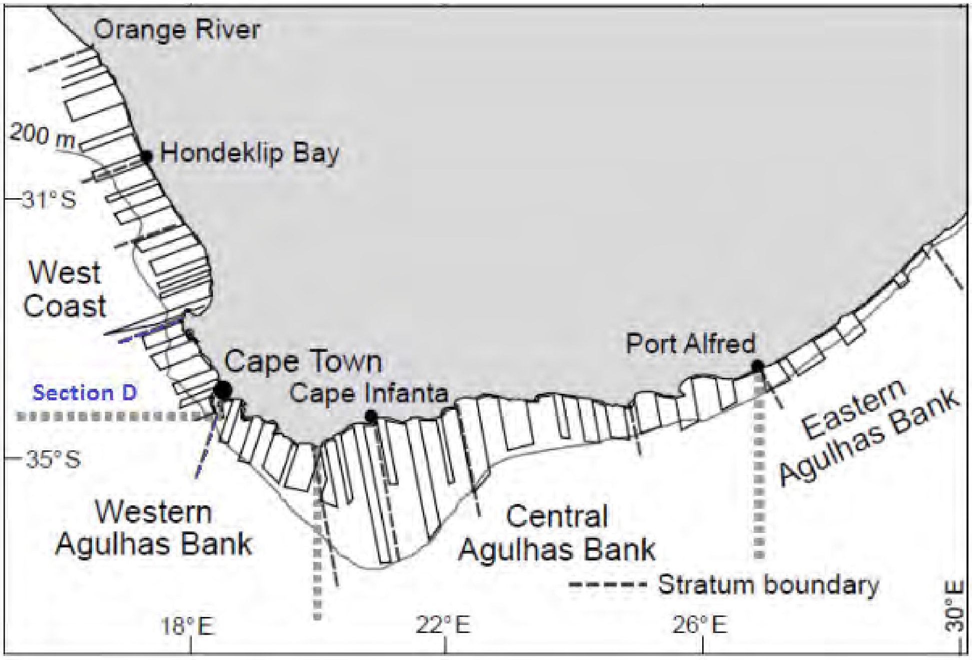


Figure 5.2 The large-scale hydro-acoustic survey transect for a typical May recruitment survey for South Africa reproduced and amended with permission from de Moor et al. (2008). Robben Island is in section D.

Simultaneous African Penguin tracking

African Penguins rearing small chicks were equipped with a Global Positioning System (GPS) and temperature depth logger devices for one foraging trip; for device and attachment details see Chapter 4. Coordinating deployments with the times of hydro-acoustic surveys was challenged by the limited weather conditions in which the hydro-acoustic surveys could take place. The protocol for equipping penguins with devices (Chapter 4) and the number of devices available limited efforts to target penguins at sea with devices. Efforts were made to have penguins at sea with devices at the time or close to when the fine-scale hydro-acoustic surveys took place.

African Penguin diet samples

Diet sampling has been conducted at Robben Island since 1989 by the Department of Environmental Affairs (DEA), Oceans and Coasts Branch, South African government (Crawford et al. 2011). Adult birds in transit back to their nests in the evening were sampled using the water-offloading technique (Wilson 1984), which involves flushing the stomach with seawater. For each diet sample obtained, prey species were identified and weighed to obtain percent mass of different prey species of the sample following Crawford et al. (2011).

Analysis

Pelagic fish hydro-acoustic survey data

The echograms collected from the hydro-acoustic surveys were analysed by DAFF. Pelagic fish density estimates per GPS survey point and total estimated abundance were conducted and provided by DAFF. First, the density of pelagic fish was calculated for each elementary sampling distance unit and then those were used to calculate the total pelagic fish abundance around the island following Jolly and Hampton (1990) methods weighting transects by weight and variance as described in Coetzee et al. (2008), de Moor et al. (2008), and Merkle et al. (2012a, 2012b). Anchovy and Sardine are not easily acoustically distinguishable and in the large-scale surveys catch composition and length frequency distributions from trawl samples in the vicinity are used for this purpose (Coetzee et al. 2008); for the small-scales fish were not distinguished beyond pelagic fish (Coetzee et al. 2008, Janet Coetzee pers. comm.). There were no catch data within 10 nautical miles (18.52 km) of the island but catches within 30 nautical miles (55.56 km) of the island indicate Anchovy was dominant (Coetzee 2014). However, due to the uncertainty estimates are for pelagic fish biomass in the 20 km radius area around the island in the upper 50 m of the water column where penguin foraging generally takes place (Merkle et al. 2012b).

African Penguin foraging behaviour

The GPS and dive data of African Penguin at sea foraging trips were analysed as described in Chapter 4. African Penguins alternate periods of traveling underwater and at the surface (Wilson 1985a). Dives were considered to be depths of 1 m or greater. Penguin dives of 3 m or greater were considered foraging dives because it is these deeper dives in which foraging generally takes place (Wilson and Wilson 1990, Pichegru et al. 2012, 2013). A linear interpolation of foraging dive locations was conducted using the GPS track and pressure data (Chapter 4). The foraging behaviours calculated per trip were foraging distance, path length and duration, time diving, vertical distance, wiggles as estimates of the number of prey captures, catch per unit effort (CPUE), total time in the bottom phase, median dive efficiency (DE) (eqn. 4.1), percentage of time diving when at sea and number of dives and foraging dives (Table 4.2). For the dive data there were multiple measurements per penguin for dive phase durations, DE and post-dive intervals (Table 4.2).

To examine penguin foraging in relation to the pelagic fish densities around the island, the distributions of pelagic fish were mapped with inverse distance weighted interpolations conducted in ArcGIS 10.3. Then, the African Penguin foraging dives for penguins which were at sea on the same day as the fine-scale hydro-acoustic survey was conducted were overlaid. The foraging dive locations of penguins foraging on the same side of the island as the side the survey was conducted that day were examined in detail to identify whether penguins foraged at specific pelagic fish densities around the island.

Secondly, I examined whether there was inter-annual variation in pelagic fish abundance around the island from the multiple fine-scale hydro-acoustic surveys conducted. Then, penguin foraging behaviour between those years for which there was evidence of differences in local pelagic fish abundance were compared. I predicted the foraging behaviour in a year of lower pelagic fish abundance would have evidence of a greater energetic and temporal investment in foraging. For the year of lower fish abundance I predicted longer: foraging distance, path length, trip duration, time diving, vertical distances and total time in the bottom phase. I predicted search times would be longer in conditions of lower prey abundance so penguins would have a lower CPUE, but a higher percentage of time diving when at sea, higher dive efficiency and make more dives and foraging dives. I predicted more wiggles (prey capture) would take place in penguin trips at times of higher fish abundance.

For the third part of my study comparing penguin foraging behaviour to different fish abundances around Robben Island there was concern about which temporal scale at which to conduct the comparison to avoid spatio-temporal mismatch. For this reason, pelagic fish shoal swimming speeds were carefully considered.

Pelagic fish shoal movements estimates to identify the extent of spatio-temporal accuracy

The swimming speeds of Anchovy and Sardine have been researched in captivity and show variation according to behavioural activity: non-feeding, particle-feeding or filter-feeding (James 1987, James and Findlay 1989, James and Probyn 1989, van der Lingen 1995). The swimming speeds are faster when feeding than during non-feeding activity for both Anchovy and Sardine (James and Findlay 1989, van der Lingen 1995). Both species feed on zooplankton but there is partitioning in the zooplankton size on which they feed, with Anchovy being more generally particle feeders and Sardine more generally filter feeders on smaller zooplankton (van der Lingen et al. 2006).

Using this information, I estimated of the minimum time it might take a shoal of Anchovy to move through the study area if they were to travel in a consistent direction and in a straight line past the island and the survey transects, a distance of c. 44 km. On the west coast of South Africa the main feeding period of Anchovy has been observed to be from 19:00 to 24:00 South Africa time zone (UTC+02:00) (James 1987), but for a conservative estimate I will assume feeding swim speeds throughout the night. Over the African Penguin breeding season the day length is on average 10.5 h. For the day of a hydro-acoustic survey shoals are traveling roughly the average non-feeding speed while at night (the following 13.5 h). the average feeding speeds are more appropriate. In this way, I estimated the minimum amount of time over which the fish abundance around the island is roughly comparable. The swimming speeds of wild Anchovy of mean (± SD) body length (BL) of 100.4 mm ± 5.9 mm have a routine mean swim speed of 1.695 ± 0.591 BL/s (17 cm/s) and a mean particle feeding speed of 2.412 ± 0.700 BL/s (24 cm/s) (James and Findlay 1989). This could amount to a distance covered of 18.3 km over 24 h. So, if traveling at those mean speeds in a straight trajectory southward it would take 2.4 periods of 24 h (or 58 h) for Anchovy to pass through the study area. As for Sardine, in captivity Sardines of average body length of 256.0 ± 9.8 mm have routine swimming speeds of 0.78 ± 0.14 BL/s (20 cm/s) while filter feeding speed ranges from 0.6 up to 2.6 BL/s (15.4 – 66.6 cm/s) (van der Lingen 1995). If the midpoint (41 cm/s) of filter feeding speeds observed is used for the speed traveled at night, that gives a possible maximum distance of 27.5 km in a period of 24 h (7.6 km per day and 19.9 km per night). So if traveling at those speeds in a straight trajectory southward it would take Sardine roughly two days (38 h) to pass through the survey area.

By these estimates, if mixed shoals travel consistently southwards in a straight trajectory it would take at least 2 days for them to travel 44 km, roughly equivalent to the distance of the survey area. The marine environment is dominated by curvilinear features and thus marine trajectories are unlikely to be linear (Tremblay et al. 2006), especially when passing through areas of predators (Wilson et al. 1987). Passes of an artificial predator caused fish shoals to depolarize frequently in captivity (Wilson et al. 1987).The maximum speed of Anchovies recorded during these consecutive artificial predator passes is 90.1 cm/s, but it could only be sustained for up to 10 to 15 seconds (James and Probyn 1989). This indicates that fish shoals do have the capacity to travel rapidly particularly in the presence of predators for short bursts, but then shoals often change direction. Also worth consideration is that fish which swim past Robben Island on the east side are likely to enter Table Bay and then have a longer route past the island. Current patterns on the west coast can lead to a retention of juveniles in particular areas (Boyd et al. 1992). It is possible there is a retention of recruits in Table Bay. Therefore, these estimates are likely to be minimum times for fish shoals to move through the study area because animal movement in nature is likely to be at intermittent varied speeds and swimming is more likely to be nonlinear as currents and water flow in the environment are likely to influence fish movements (Dickinson et al. 2000, Tremblay et al. 2006).

Field observations of pelagic fish shoals at sea put swimming speeds at much higher estimates of 9 km/h for Anchovy adults from fishermen in relation to boat speeds (Wilson 1985b). If that is the case, shoals could potentially pass through the study area in a minimum of 5 h if traveling in a straight trajectory. On the other hand, Waller (2011) estimates recruit southward movements of 2 km/day, from using estimates of the distance traveled from Orange River to the Agulhas Bank a distance of c. 400 km and the timeframe of six months over which the journey is thought to take place. From this estimate shoals would move through the study area in 22 days. Other estimates which consider the southward recruit shoal movement to be proportional to movement of the current and zooplankton have bound the southward shoal speed or recruits at speeds between 10-20 km/day (Hutchings 1992). For models investigating Anchovy foraging and copepod dynamics the bounds for the maximum daily distance traveled by Anchovies is 15 km/day (Plagányi 1995, Plagányi et al. 2000). If traveling at that maximum distance consistently southwards shoals would pass the survey area in a minimum of 2.9 days.

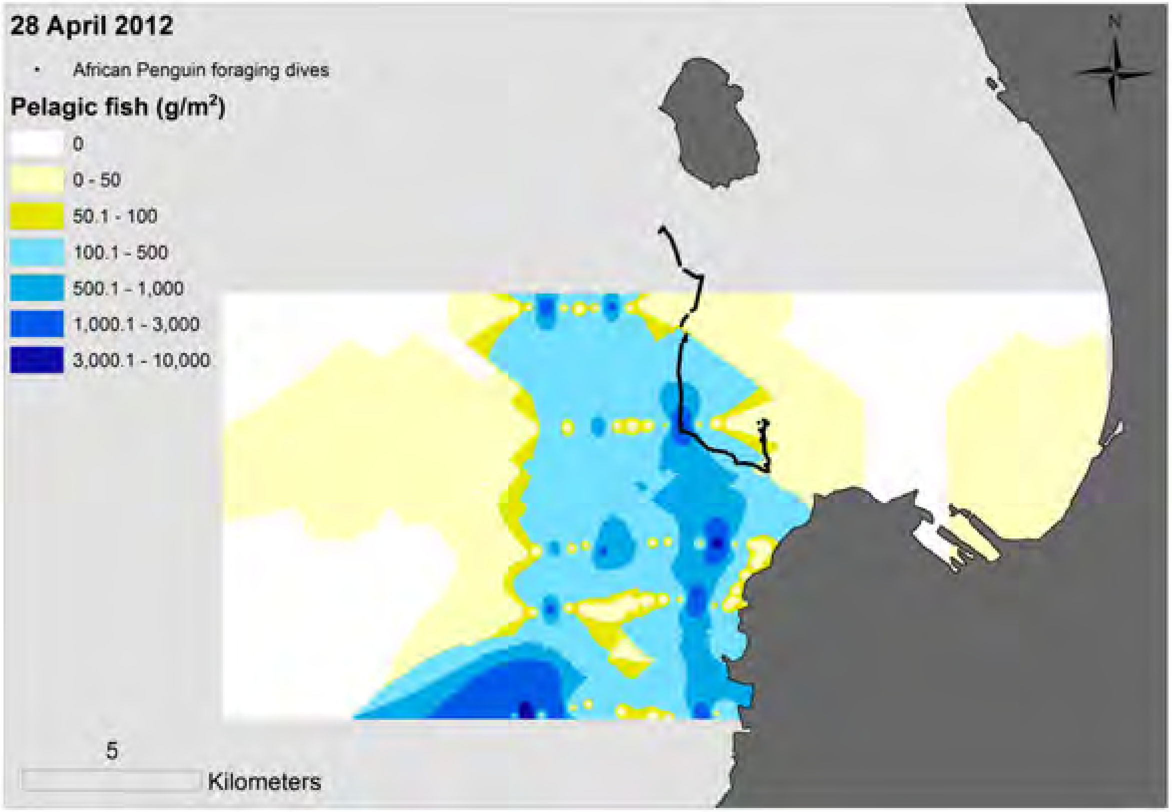
For the purposes here of identifying the timeframe within which pelagic fish estimates are likely to be comparable to penguin behaviour, I used the intermediate and conservative estimate of within 2 days of a survey.

Penguin foraging behaviour in comparison to local prey abundance

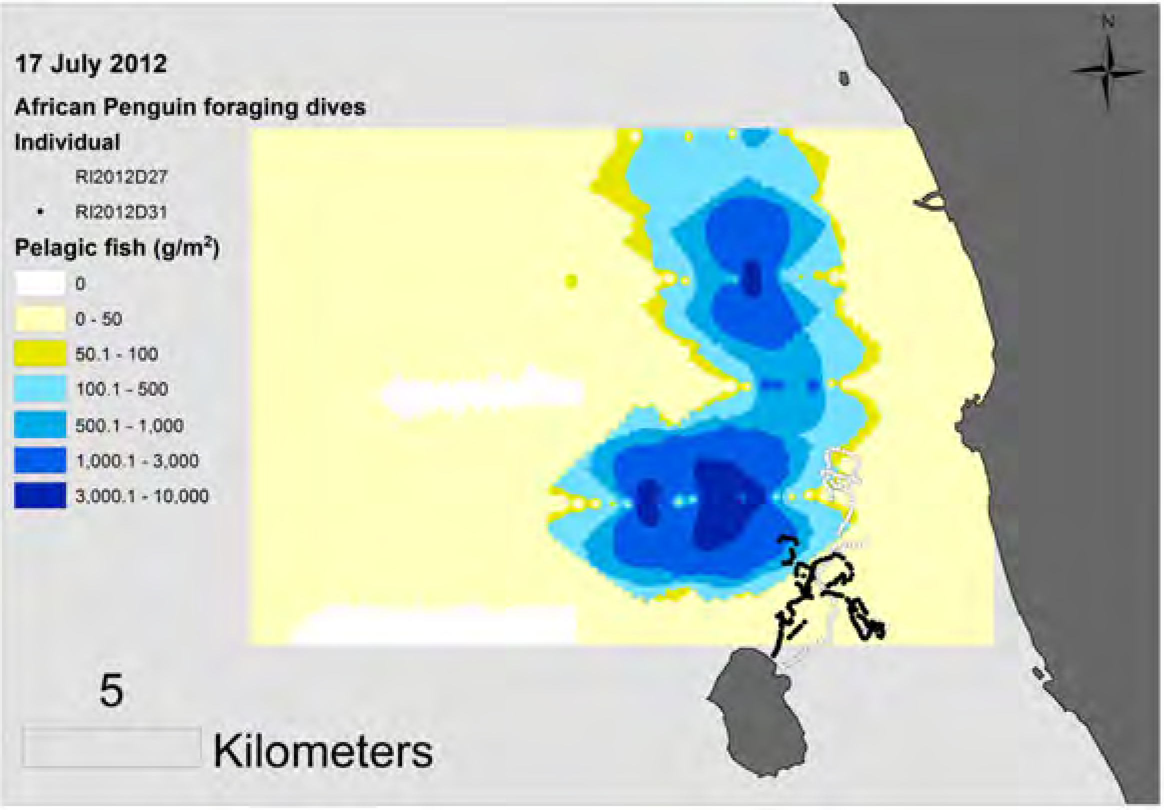
The relative influence of prey abundance around the island as an extrinsic factor on foraging behaviour was investigated with principal components analysis, in the same way the extrinsic factors of sea conditions and intrinsic factors were investigated in Chapter 4. PCA variable factor maps were plotted to assist in identification of relationships between each supplementary variable of interest and the foraging behaviour measures (following Zimmer et al. 2010). The foraging behavioural measures were: foraging distance from the colony, total time diving, median dive depth, number of dives, mean bottom phase duration, and total number of wiggles. These were calculated for the penguins at sea within 2 days of a survey. Sample sizes were small so data from all years were combined. The estimated abundance of pelagic fish was added as a supplementary variable of interest to identify any strong relationships with the foraging behavioural measures. The PCA was performed in R with the 'PCA' function in FactoMineR package (Husson et al. 2015). Any correlations were further investigated with regressions. In the case of heteroscedasticity in the data, quantile regressions were also performed.

Results

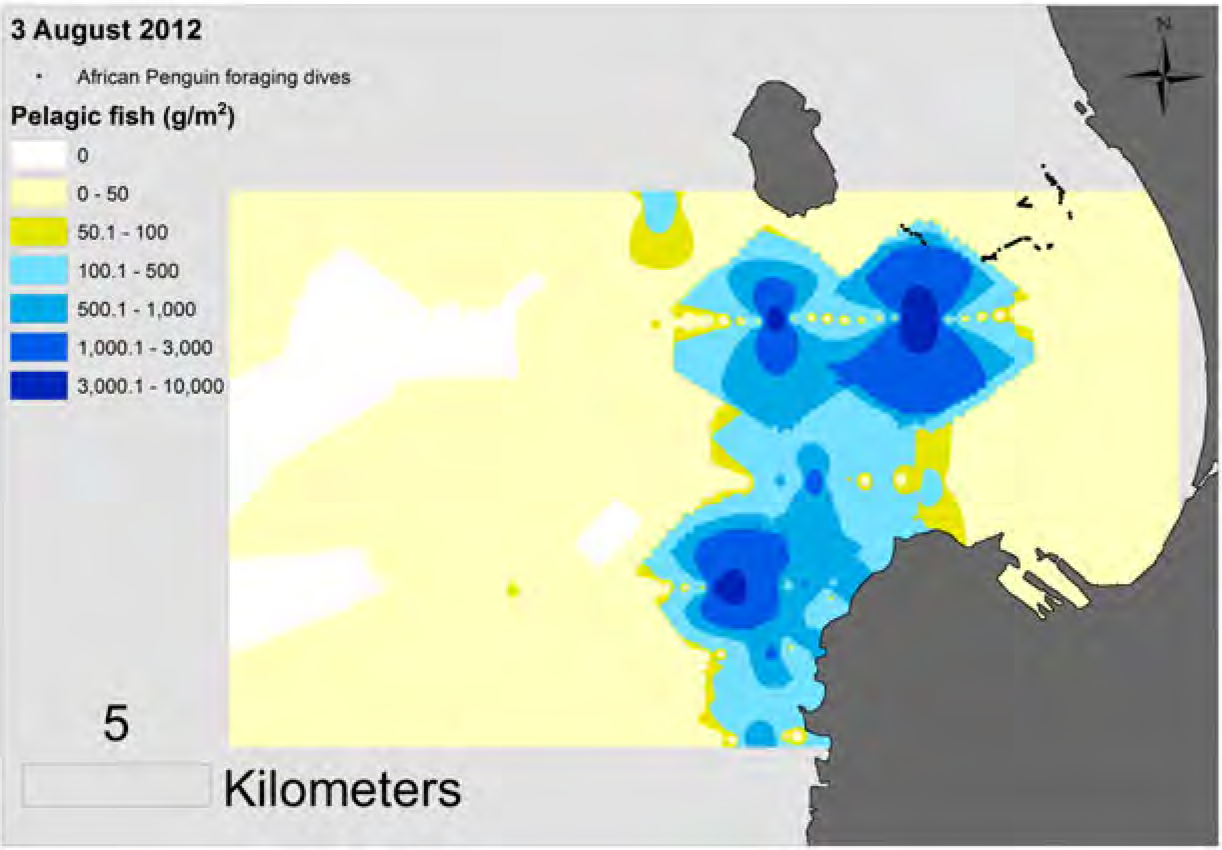
There were 30,171 African Penguin dive records and only 252 (0.8%) of those were deeper than 50 m so the assumption that the penguins were foraging in the top 50 m of the water column was accurate. During the study, four African Penguins equipped with devices were at sea on the same day and side of the island as the fine-scale hydro-acoustic survey, 16 penguins tracked within 2 days of a survey (but two had incomplete GPS data sets), and 54 penguins collected complete dive data within the same month as a survey. On three survey days there were penguins tracked that were on the same side of the island as the hydro-acoustic survey taking place that day. Those penguins made foraging dives at pelagic fish densities ranging from 1 g/m^2 to 3,000 g/m^2. African Penguins appeared to forage on the edges of the densest areas of fish (Fig. 5.3).


28 April 2012
African Penguin foraging dives
Pelagic fish (g/m²)
0
0 - 50
50.1 - 100
100.1 - 500
500.1 - 1,000
1,000.1 - 3,000
3,000.1 - 10,000
5
Kilometers
N

A


17 July 2012
African Penguin foraging dives
Individual
RI2012D27
RI2012D31
Pelagic fish (g/m²)
0
0 - 50
50.1 - 100
100.1 - 500
500.1 - 1,000
1,000.1 - 3,000
3,000.1 - 10,000
5
Kilometers
N

B



C

Figure 5.3. Maps of the pelagic fish density (g/m^2) around Robben Island from three hydro-acoustic surveys with African Penguin foraging dives when: (A) one penguin was at sea the same side of the island as on the second day of the survey in April 2012, (B) two penguins were at sea the same day and same side of the island the first day of the survey in July 2012, and (C) when one penguin was at sea the same day and side of the island as the second day of the survey that took place in August 2012.

Fine-scale hydro-acoustic surveys around Robben Island showed the local prey abundance is highly variable. A total of 12 surveys were conducted during the African penguin breeding season and the mean ± SE of pelagic fish biomass around the island was 50,915 ± 17,887 t (range: 549 – 187,249 t) (Table 5.1). There was evidence from the fine-scale hydro-acoustic surveys that took place that the pelagic fish abundance was distinctly higher in 2012 (median 72,711 t) than it was in 2011 (median 5,981 t) (Fig. 5.4). Furthermore, the recruitment biomass of the large-scale survey and section that Robben Island falls under (Section D: Cape Columbine to Cape Point) were higher in 2012 than 2011 (Table 5.2). In 2013, only one hydro-acoustic survey around the island was conducted and indicated low pelagic fish abundance around the island in May while the large-scale survey also conducted in May for that section indicated a high relative abundance (Table 5.1, Table 5.2). This demonstrates how the large-scale abundance may not always be representative of the local fine-scale abundance.

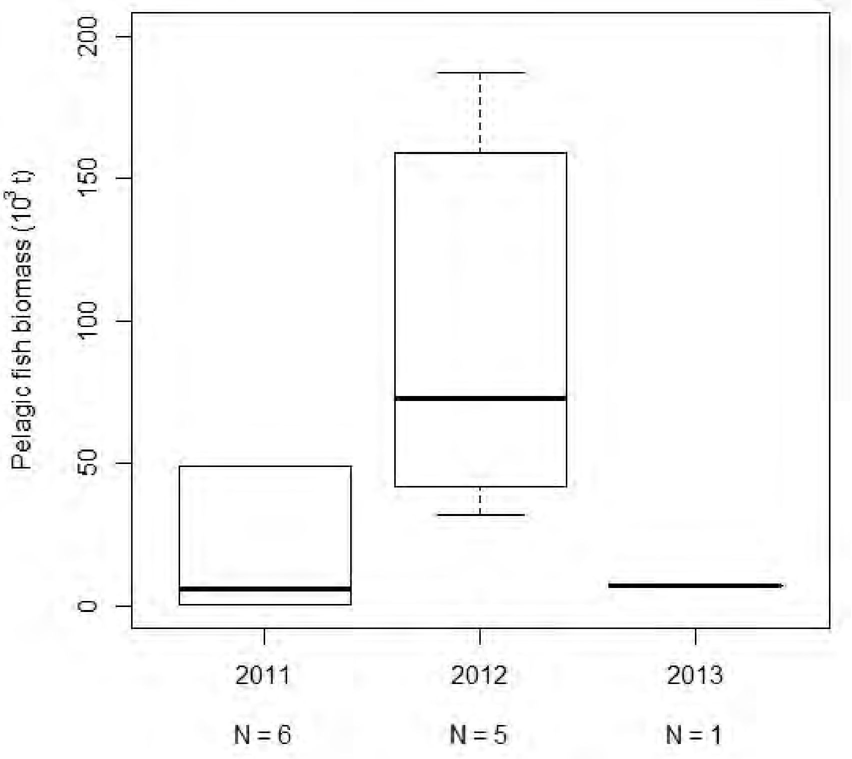


Figure 5.4. Box and whisker plots of the estimates of pelagic fish biomass (10^3 t) around Robben Island from fine-scale surveys conducted in the years when simultaneous African Penguin tracking took place. The number of surveys conducted are provided under the year. The midline is the median, the box extends to the lower and upper quartiles and the whiskers extend to the the range of the data.

Table 5.1. Fine-scale hydro-acoustic surveys conducted around Robben Island from 2011 to 2013 during the African Penguin breeding season and the total pelagic fish biomass estimates (Merkle et al. 2012a, 2012b, Coetzee 2014).

Year	First survey day	Last survey day	Month	Pelagic fish biomass (t)
2011	08-March	10-March	March	49,289
2011	16-May	17-May	May	4,406
2011	27-June	28-June	June	48,962
2011	26-July	27-July	July	549
2011	16-August	17-August	August	7,556
2011	26-September	27-September	September	657
2012	26-March	27-March	March	41,705
2012	27-April	28-April	April	72,711
2012	17-July	18-July	July	159,039
2012	02-August	03-August	August	187,249
2012	05-September	06-September	September	31,693
2013	15-May	16-May	May	7,159

Table 5.2. Large-scale hydro-acoustic survey of pelagic fish recruitment biomass in tonnes (t) and coefficient of variation (CV) in May/June along the South African coastline from Orange River to Cape Infanta and for the survey section where Robben Island is situated, section D which is from Cape Columbine to Cape Point. Estimates of the numbers of recruits were available for the total survey (Mhlongo et al. 2012, Phillips et al. 2013, DAFF unpublished data).

		West coast recruitment survey					
		Entire coast (Cape Infanta to Cape Point)			Section D (Cape Columbine to Cape Point)		
		Year			Year		
		2011	2012	2013	2011	2012	2013
Anchovy	Biomass (t)	281,260	990,378	1,164,278	12,118	92,328	373,178
	CV	0.283	0.138	0.182	0.53	0.538	0.34
	No. recruits (billions)	104.17	210.56	352.99			
Sardine	Biomass (t)	53,681	86,089	102,169	215	397	87,252
	CV	0.235	0.321	0.416	0.801	0.497	0.48
	No. recruits (billions)	5.47	8.1	12.12			

Breeding African Penguin diet composition at Robben Island varied between the years of the study; in 2011 the lowest average percent mass of Anchovy (36%) was recorded while in 2012 and 2013 Anchovy mass contributions were more typical at 97% and 93%, respectively. Prior to 2011 Anchovy percentage was typically greater than 70%, the average being 83% and minimum 55% (Crawford et al. 2011). In 2011, Cape Horse Mackerel (*Trachurus trachurus capensis*) which is 0.38 kJ/g less energy than Anchovy (Balmelli and Wickens 1994), made up to 50% of the diet mass (Table 5.3).

Table 5.3. Annual African Penguin prey items mass (%) in diet samples taken at Robben Island from 83 individuals when there was a purse-seine fisheries closure in place out to 20 km around the island (Source: DEA unpublished data). The sample size numbers refer to the number of individuals sampled that year.

Prey items		**Year**		
		2011 (N = 44)	2012 (N = 15)	2013 (N = 24)
Species	Group			
Anchovy *Engraulis encrasicolus*	Fish	37.65	97.45	93.48
Cape Horse Mackerel *Trachurus trachurus capensis*	Fish	50.59	0.31	0.85
Round Herring *Etrumeus whiteheadi*	Fish	3.72		
Beaked Sandfish *Gonorynchus gonorynchus*	Fish	3.15	2.24	0.16
Southern Mullet *Liza rchardsonii*	Fish	2.17		
Longsnout Pipefish *Syngnathus acus*	Fish	0.36		1.19
Klipfish *Genypterus capensis.*	Fish	0.16		0.34
Pike *Esox* spp.	Fish	0.01		
Eel unidentified	Fish			
Larval fish unidentified	Fish	0.48		
Thumbstall Squid *Lolliguncula brevis*	Squid	0.98		0.76
Lesser- flying Squid *Todaropsis eblanae*	Squid	0.22		
Angola-flying Squid *Todarodes angolensis*	Squid	0.05		
Bobtail Squid unidentified *Loligo spp.*	Squid	0.04		
Chokker Squid *Loligovulgaris reynaudii*	Squid			1.41
Squid unidentified *Loligo spp.*	Squid	0.02		0.64
Blue Coral-worm *Plomatoleios kraussii*	Annelid	0.13		
Mantis Shrimp *Pterygosquilla armata capensis*	Arthropod	0.12		
Unidentified	Unidentified	0.17		0.50

Comparing the foraging behaviour collected between those two years with Welch's t-tests because samples sizes were small showed foraging effort measures were significantly higher in 2011, when prey abundance was lower (Table 5.4). Measures were as predicted except for wiggles and CPUE. Contrary to expectation, wiggles per trip were higher in 2011 when there was a lower abundance of pelagic fish but the CPUE did not differ between years (Table 5.4). This indicates that while more prey captures occurred in 2011 birds were not capturing more per unit of time foraging than they were at times of higher pelagic fish abundance in 2012. There was a positive correlation between the number of wiggles in a trip and the total time a penguin spent diving ($r = 0.74$, $t_{72} = 9.39$, $p < 0.001$), yet heteroscedasticity increased with increasing time diving (Fig. 5.5). Considering more than half of prey items were lower in calorific content in 2011 than in general, it makes sense that more prey had to be captured for a penguin to capture a prey load of equivalent energetic content.

Table 5.4. Comparison of the foraging behaviour of 64 African Penguins provisioning for small chicks at Robben Island at years of distinctly low and high pelagic fish abundance.

	Relative pelagic fish prey abundance			
	Low biomass 2011	High biomass 2012		
Penguin foraging behaviour measure	Mean ± SE (range) N	Mean ± SE (range) N	Average difference (95% CI)	Welch's t-test
Trip duration (h)	16.2 ± 3.3 (8.7 − 42.9) 27	10.9 ± 1.0 (7.4 − 25.4) 37	5.3 (1.1 − 9.6)	$t_{29.3}$ = 2.6, p = 0.014
Path length (km)	56.1 ± 11.4 (23 − 158.3) 25	34.3 ± 2.9 (14.2 − 59.2) 35	21.8 (6.4 − 37.3)	$t_{25.1}$ = 2.9, p = 0.008
Foraging distance (km)	15.5 ± 3.3 (6.0 − 47.7) 25	8.9 ± 0.9 (3.8 − 15.5) 35	6.6 (2.1 − 11.0)	$t_{25.1}$ = 3.0, p = 0.006
Total time diving (h)	7.1 ± 0.9 (3.3 − 13.5) 26	4.4 ± 0.3(1.9 − 5.9) 37	2.7 (1.6 − 3.9)	$t_{29.3}$ = 4.7, p < 0.001
Vertical distance (km)	14.8 ± 2.0 (6.9 − 29.8) 26	9.9 ± 1.0 (2.5 − 15.3) 37	4.9 (2.1 − 7.6)	$t_{33.3}$ = 3.6, p = 0.001
Total bottom phase time (h)	2.4 ± 0.4 (0.9 − 5.6) 26	1.2 ± 0.1(0.4 − 2.3) 37	1.2 (0.8 − 1.7)	$t_{30.3}$ = 5.4, p < 0.001
Median DE	0.22 ± 0.2 (0.14 − 0.36) 26	0.15 ± 0.02 (0.03 − 0.30) 37	0.07 (0.04 − 0.11)	$t_{48.1}$ = 4.5, p < 0.001
Percent of time at sea diving (%)	48 ± 3 (28 − 64)26	41 ± 3 (21 − 64) 37	7 (1 − 12)	$t_{55.5}$ = 2.4, p = 0.020
No. dives (depth > 1 m)	487 ± 59 (234 − 1008)26	330 ± 29 (213 − 574) 37	157 (76 − 238)	$t_{33.5}$ = 4.0, p = 0.0003
No. Foraging dives (depth > 3 m)	411 ± 52 (216 − 894) 26	256 ± 26 (106 − 497) 37	155 (84 − 227)	$t_{33.8}$ = 4.4, p < 0.001
No. Wiggles	267 ± 39 (52 − 752) 26	104 ± 10 (25 − 258) 37	163 (79 − 247)	$t_{28.4}$ = 4.0, p < 0.001
CPUE	1.7 ± 0.2 (0.5 − 3.7) 26	1.5 ± 0.1 (0.4 − 2.9) 37	0.2 (-0.09 − 0.65)	$t_{47.8}$ = 1.5, p = 0.130

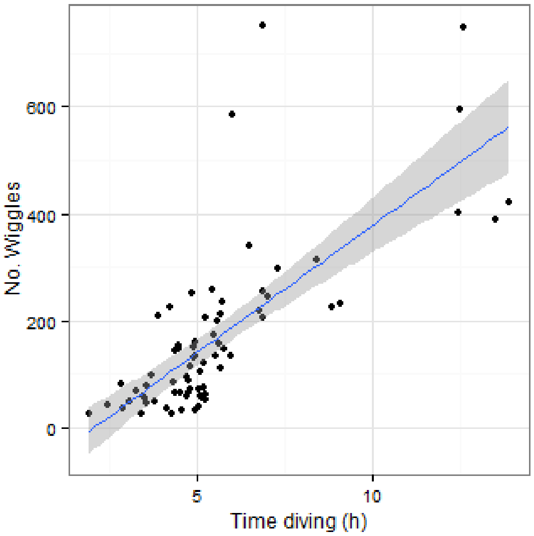


Figure 5.5. The number of wiggles made by African Penguins on a foraging trip rearing small chicks as explained by total time spent diving (h) with a linear regression line and 95% confidence intervals. The outlying numbers of wiggles greater than 500 are from 2011.

Diet composition differed in 2011 when the abundance of pelagic fish was particularly low. Therefore, there is a possibility that the relationships observed could be due to differences in behaviour when foraging for different prey types. To try to control for diet composition, I investigated foraging behaviour within 2012. The percentages of Anchovy in the diet samples taken in 2012 were all over 90% in May (99.85%), June (99.78%) and July (92.7%). The April hydro-acoustic survey and penguin deployments took place late in the month close to when the diet sampling occurred in early May. The relative pelagic fish abundance around the island in July was 86,328 t more than in April (Table 5.1). Thus, an exploratory comparison was conducted between the foraging behaviour of 16 penguins foraging in July and the four penguins at sea in late-April with Welch's *t*-tests as sample sizes were small. In April, when fish abundance was lower the penguins traveled on average 2.3 km (95% CI: 0.1–4.5 km) further from the island ($t_{5.26}$ = 2.70, p = 0.04), made on average 189 (95% CI: 37–341) more foraging dives ($t_{3.33}$ = 3.75, p = 0.03), and their median dive efficiency was on average 0.1 (95% CI: 0.04–0.16) higher ($t_{5.60}$ = 3.96, p = 0.009). Those were the only significant results and while they are not conclusive as sample sizes were small they also indicate that foraging effort was higher when fish abundance was lower, which is consistent with our predictions. The other behavioural parameters including the number of wiggles were not significantly different (p > 0.05). This indicated the number of prey captures necessary and acquisition rates are similar when prey type is consistent.

The investigation into the influence of pelagic fish abundance with the foraging behaviour of 14 penguins at sea within two days of a fine-scale fish survey by principal components analysis showed that pelagic fish biomass estimates were negatively correlated with the time penguins spent diving, the total number of wiggles per trip and the foraging distance traveled (Fig. 5.6). Linear regressions with these factors showed local prey abundance explained more than half of the variation in time diving, with adjusted R^2 value of 0.60 ($F_{1,12} = 19.86$, $p < 0.001$), and some of the variation in the numbers of wiggles and foraging distance travelled with adjusted R^2 values of 0.45 ($F_{1,12} = 11.43$, $p = 0.005$) and 0.27 ($F_{1,12} = 5.93$, $p = 0.03$) respectively (Fig. 5.7). However, the data showed heteroscedasticity so the 10% and 90% quantiles were also conducted to investigate the maximum and minimum responses in behaviour to local pelagic fish abundance (Fig. 5.7). There was a greater range in foraging distance travelled and the number of wiggles per trip when local pelagic fish biomass was low (Fig. 5.7), this indicates different foraging strategies when biomass is low. I also conducted these analyses for penguins at sea with devices in the same month of a fine-scale surveys and the patterns observed held when there was greater temporal noise but the pelagic fish abundance explained less of the variability in behaviour as would be expected as there would be more temporal spatial mis-match.

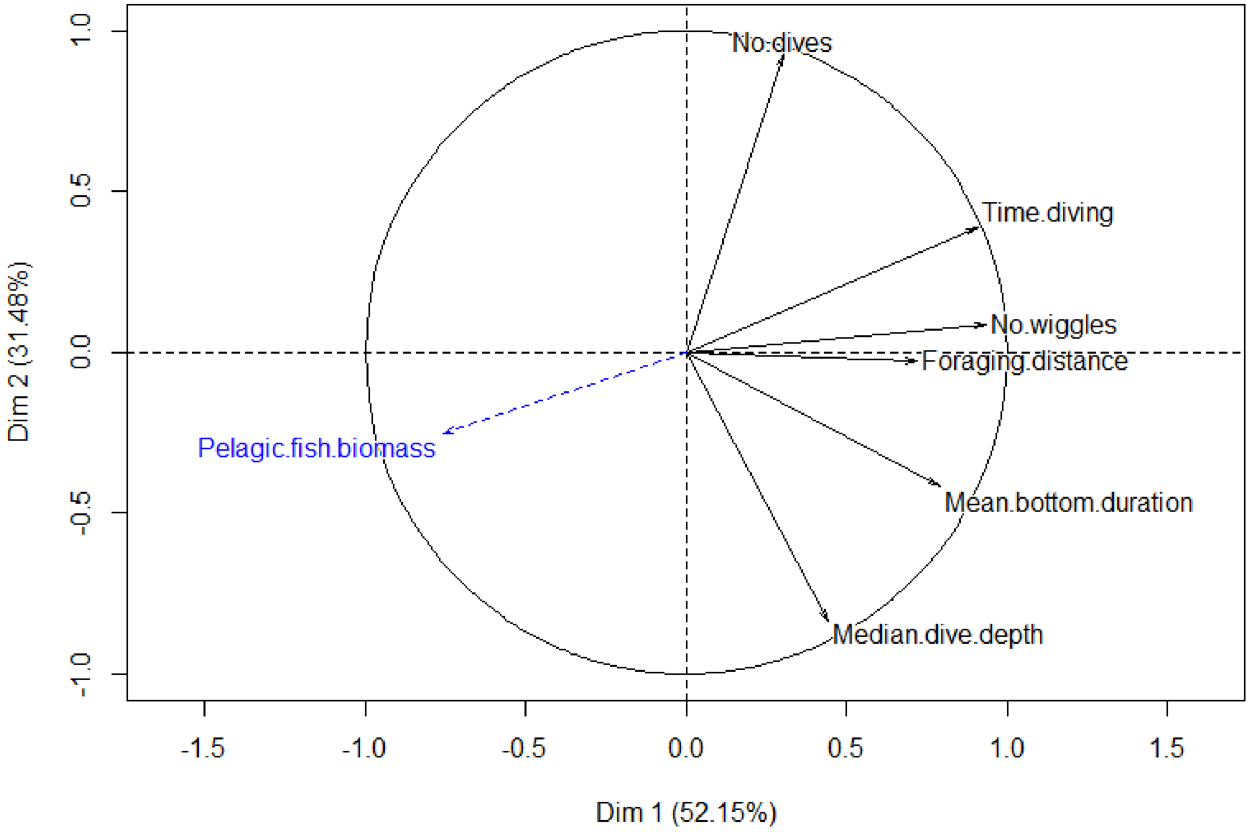


Figure 5.6. Variables factor map of principal component analysis (PCA) for behavioural foraging measures of 14 breeding African Penguin at sea within at least two days of a fine-scale hydro-acoustic survey (N = 5) that had complete data sets with the supplementary variable of interest, the estimated pelagic fish biomass around the island, shown as a blue arrow with a dashed line. The distance and direction of the arrow indicates a strong negative influence to the behavioural measures. The pelagic fish biomass was most strongly correlated to the time penguins spent diving (r = −0.79 [95% CI: −0.44 to −0.93], t_{12} = 4.46, p < 0.001). It was also negatively correlated to: the number of wiggles (r = −0.70 [95% CI: −0.27 to −0.70], t_{12} = 3.38, p = 0.005) and the maximum distance traveled (r = −0.58 [95% CI: −0.06 to −0.85], t_{12} = 2.44, p = 0.03). Correlations of the pelagic fish biomass to median bottom phase duration, median dive depth and total dive number were negative but not significant.

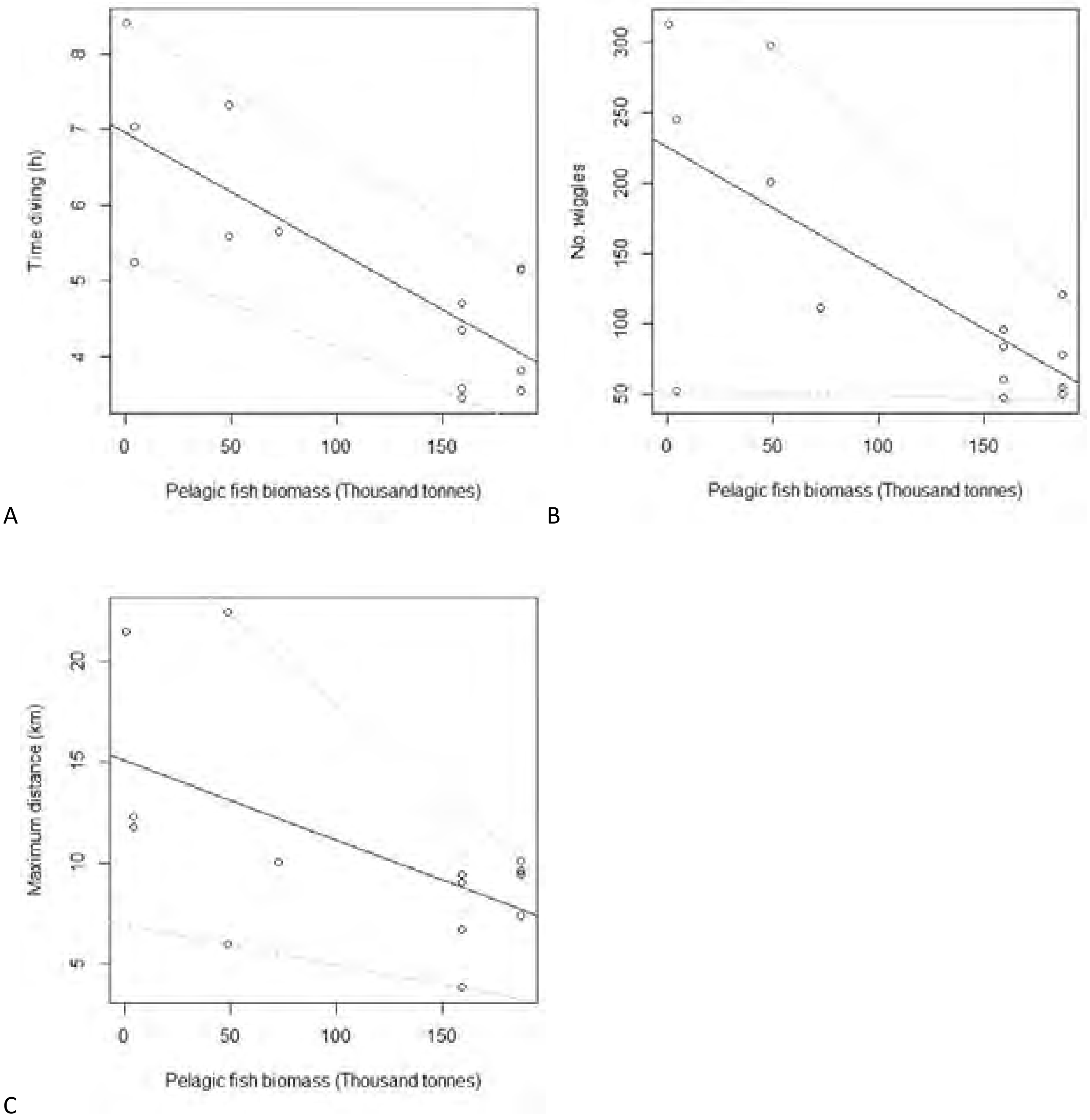


Figure 5.7. The foraging behaviours of 14 African Penguin as explained by the pelagic fish abundance estimated around Robben Island (10^3 t) from five hydro-acoustic surveys. The penguins were at sea within two days or less of a survey. The solid lines shows the linear regression line while the grey dashed lines show the 90% and 10% quantile lines for (A) time diving (regression line: $y = -0.0156x + 6.96$, 90% quantile: $y = -0.0173x \pm 8.41$ and 10% quantile: $y = -0.0116x \pm 5.29$), (B) the number of wiggles per trip (regression line: $y = -0.861x \pm 226$, 90% quantile: $y = -1.28x \pm 361$and 10% quantile: $y = -0.0323x \pm 52.1$) and (C) foraging distance (regression line: $y = -0.0396x \pm 15.1$, 90% quantile: $y = -0.0892x \pm 26.8$and 10% quantile: $y = -0.0196x \pm 6.91$).

Discussion

This investigation pioneers the exploration of African Penguin foraging behaviour with GPS temperature depth tracking devices in combination with fine-scale hydro-acoustic pelagic fish survey around island colonies. African Penguins forage in a variety of pelagic fish densities around Robben Island and appear to forage on the edge of the highest pelagic fish densities (Fig. 5.3). Foraging effort was higher in 2011 when local preferred pelagic prey was at lower abundance than in 2012 (Table 5.4). African Penguins spent more time diving for prey items and travel further when pelagic fish were lower in abundance around the penguin colony (Fig. 5.6, Fig. 5.7). These findings give support to the assumption of Petersen et al. (2006) that African Penguin behavioural provisioning measures indicate local prey availability. These findings are consistent with other seabird studies where at times of lower prey abundance provisioning trips were of longer duration (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Kadin et al. 2012), covered greater distances (Monaghan et al. 1994, Burke and Montevecchi 2009), and consisted of longer times diving (Monaghan et al. 1994). Furthermore, penguin studies that compared foraging behaviour in areas that differed in prey availability (Hennicke and Culik 2005, Wilson et al. 2005) and productivity (Boersma et al. 2009), also found trip distances were longer in areas of lower prey availability. While responses from different species to prey availability can be varied (Baird 1990, Furness and Camphuysen 1997, Sabarros et al. 2012), the overall behavioural patterns in foraging effort of central place foragers to prey abundance appear to be similar.

There is the possibility that differences in diet composition had a confounding effect. The high percentage of Cape Horse Mackerel observed in the diet samples in 2011 (Table 5.3), indicates there was low availability of preferred prey (Anchovy) that year. However, comparisons within 2012 when diet composition was consistent (Table 5.3), found evidence of higher foraging effort when prey abundance was lower as expected. However, sample sizes were small so further investigation is recommended. African Penguins appear to adjust their behaviour at sea depending on prey availability as does the Magellanic Penguin (*S. magellanicus*) (Wilson et al. 2005, Boersma et al. 2009, Sala et al. 2014). The number of wiggles can be interpreted to be representative of the number of prey captures (Simeone and Wilson 2003, Sala et al. 2012). Applying this interpretation to our results indicates the number of prey caught increased with lower prey abundance, contrary to expectations. However, it was explained by the low percentages of Anchovy in the diet in 2011 when pelagic fish abundance was lower. If prey types are lower in energy content or smaller more would need to be caught to acquire an equivalent energy content. The within-year behavioural comparison at times of different relative pelagic prey abundance but comparable high compositions of Anchovy found prey capture numbers were similar.

The observation of a typically specialist seabird switching to other prey types at times of low abundance has also been found in Common Murres (*Uria aalge*) (Burger and Piatt 1990). While the change in diet of African Penguins at Robben Island observed was short-term, a more long-term diet shift has taken place in African Penguins in Namibia (Ludynia et al. 2010). There was a regime shift when pelagic fish stocks collapsed in the 1970s (Cury and Shannon 2004) and Bearded Goby (*Sufflogobius bibarbatus*), a fish of lower energetic value than Anchovy or Sardine, has become dominant in the Namibian African Penguin diet (Ludynia et al. 2010). African Penguins have some flexibility in diet but the low prey quality in Namibia is considered to have contributed to population declines (Kemper et al. 2001, Kemper 2006, Ludynia et al. 2010). There is evidence lower prey availability has population effects in the African Penguin (Sabarros et al. 2012, Sherley et al. 2013) but whether it impacts chick condition will be addressed in the next chapter.

Previous large-scale investigations using GPS tracking and hydro-acoustic surveys to investigate overlap between top predators and prey found evidence of spatial match-mismatch between Cape Gannet foraging zones and pelagic fish densities (Grémillet et al. 2008). That penguins foraged on the edges of high prey density suggests such patterns of match-mismatch may also be the case in African Penguins. Despite our efforts to reduce the scale at which error could occur, it is still a concern but it is likely to be small and at the scales of hours and kilometers.

At the temporal scale I addressed, penguins being 2 days within a survey, the sample sizes were too small to investigate biomass as an explanatory factor of bottom duration or DE with linear mixed effect models. These dive measures were significantly different between years (Chapter 4). The longer bottom phase durations in 2011 that increased dive efficiency that year (Table 4.8, Fig. 4.11),are likely to be explained by the low pelagic fish biomass during surveys that year. When pelagic fish biomass was lower African Penguins were more opportunistic feeders. Other prey types may require longer prey pursuits underwater than when feeding on shoals of pelagic fish. Adélie Penguin foraging did not differ in bottom phase when different prey types. It is possible dive shape varies with prey type as has been shown with Thick-billed Murres (*Uria lomvia*) which generally catch pelagic items during V-shaped dives and more benthic prey items during U shaped dives (Elliott et al. 2008). More U-shaped dives than V-shaped dives would result in longer bottom phase time. Cape Horse Mackerel have higher records of maximum swim speeds 2.82 BL/s which translates to 87 cm/s for adults and can sustain them for longer than Anchovy (James and Probyn 1989, Wardle et al. 1996); it might take penguins slightly longer to capture Cape Horse Mackerel recruits. On the other hand, penguins with diet samples that vary in prey composition can have similar bottom phase time and percentages of time spent bottom phase over the trip duration (Ropert-Coudert et al. 2002). It is also possible that a difference in prey distribution influenced diving behaviour.

Investigations into the spatial dynamics could be improved by incorporating prey aggregation information and bathymetry to derive volumetric prey densities (Benoit-Bird et al. 2013). Considering, penguins are searching for prey in a 3D marine environment volumetric density investigations would be more appropriate approach to understand these predator-prey spatial dynamics.

The heterogeneity in the foraging behavioral responses in relation to pelagic fish abundance (Fig.5.6) was an unexpected finding. It appears that there are more foraging strategies when prey abundance is low probably with some birds putting more effort into foraging than others. It is possible the variation in responses could be due to individual differences, with individuals responding to environmental conditions differently, as have been found in Northern Gannets (*Morus bassanus*) (Patrick et al. 2014). It is also possible that cognition such as memory plays a role in foraging decisions as appears to be the case in Common Murres (Regular et al. 2013). Considering the variable nature of prey abundance around the island (Table 5.1), this leads one to hypothesise that when local prey abundance is particularly low penguins are faced with the decision to either make foraging trips requiring higher energetic input to catch the amount of prey needed to sustain themselves and their chicks or gather less and wait for conditions to improve.

Conclusions

Fine-scale hydro-acoustic surveys have shown the abundance of Anchovy and Sardine around Robben Island is highly variable within and between years. This exploration of breeding African Penguin foraging behaviour in relation to prey indicates foraging effort was higher with a lower abundance of preferred prey around the colony. Foraging behaviours were negatively correlated with the estimated prey abundance around the colony. There is evidence that foraging behaviour was influenced by local pelagic fish abundance. The approach of combining seabird foraging tracking with hydro-acoustic surveys at fine-scales has potential to provide more answers to predator-prey dynamics of seabirds and small pelagics; such information makes valuable contributions to ecosystem-based fisheries management.

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Chapter 6

Chick body condition in relation to a parent's foraging behaviour, parental body condition and local pelagic fish availability

Examining chick body condition of endangered African Penguins (*Spheniscus demersus*) in relation to provisioning, diet and prey abundance can inform ecosystem management. The chick body condition index was extended to include small-sized chicks (head length < 75 mm) using non-linear quantile regressions. Concurrent monitoring of chick body condition, diet sampling and pelagic fish abundance estimated with fine-scale hydro-acoustic surveys took place at the Robben Island colony. There were 123 chicks which had a parent that was equipped with a GPS temperature depth device for one foraging trip. Chick body condition was compared to the parent's foraging behaviour, and the body condition of both parents. Linear mixed effects modelling was used to investigate whether local prey abundance and diet composition explained chick body condition at the Robben Island colony. Chick body condition was not related to the foraging behaviour measures of a foraging trip from one parent. From 2010 to 2013, 801 chicks were measured within 14 days of 13 hydro-acoustic surveys. Chick body condition was positively related to the estimated prey abundance around the island. The model predicted a 245% increase in chick body condition in the colony over the range of the pelagic fish abundance observed. From 2008 to 2013, 2,220 chicks were measured in 24 months when diet sampling was conducted. There was evidence that chick body condition increases with Anchovy (*Engraulis encrasicolus*) percent mass in the diet. These findings provide further evidence of the importance of the local prey resources for penguin colonies.

Introduction

Life-history theory predicts long-lived birds have to balance the trade-off between reproductive costs with self-maintenance and future reproduction (Erikstad et al. 1998). For polyphagous birds there can be trade-offs between provisioning quality prey items and an abundance of items (Wright 1998). At times of food shortage parents are predicted to provide less food items or food of lower nutritional quality to maintain chick survival. The functional relationships of seabirds to prey variability warrant investigation (Cairns 1988, Piatt et al. 2007). Seabirds adjust their parental effort according to their own body condition (Erikstad et al. 1997; Ballard et al. 2010, Jacobs et al. 2013). They can buffer chick survival with flexible time activity budgets (Burger and Piatt 1990, Litzow and Piatt 2003, Harding et al. 2007) or by making trips of bimodal durations (Granadeiro et al. 1998; Weimerskirch et al. 2003; Saraux et al. 2011), but there are limits to the extent seabirds can buffer using parental time budgets and chick feeding rates when prey abundance is chronically low (Harding et al. 2007). There can be confounding variables influencing reproductive success from predation and fisheries (Regehr and Montevecchi 1997). In the face of varied environmental conditions, there can be trade-offs in parental provisioning strategies (Watanuki et al. 2002, Ballard et al. 2010).

the African Penguin is currently classified as 'Endangered' under IUCN (BirdLife International 2013). There is an urgent need for an exploration of the links between fish availability, and chick and adult body condition as well as provisioning behaviour. in order to understand the population dynamics. One of the missing pieces of information is how the at-sea prey abundance affects penguin colony dynamics. How do we measure the impact in the colony to at-sea prey abundance? Chick body condition is assumed to be related to prey availability (Waller 2011, Lubbe et al. 2014). It may be more sensitive to prey availability than parental provisioning behaviour because it responds over a slightly longer timeframe. The amount of prey a breeding adult returns to the nest is related to the size of their chicks (Wilson et al. 1989). Considering this and life history theory it seems likely adults with chicks in better body condition are providing more more prey per feed or higher quality prey per feed or more frequent feeds. I hypothesise chick body condition would increase with with higher the parents' body conditions, lower parental foraging effort, increase with local availability of prey and increase with the percentage of Anchovy in the diet.

Changes in breeding success and population numbers of African Penguins have been linked consistently to the regional abundance of Sardine (*Sardinops sagax*) (Crawford et al. 2006, Sherley et al. 2013). At a local level, purse seine fisheries catch of Anchovy (*Engraulis encrasicolus*) has been linked to

African Penguin breeding success and fledging rates at Robben Island (Sherley et al. 2013). For breeding success, African Penguins require adequate regional supplies during non-breeding and adequate local food supplies during breeding (Sherley et al. 2013).

Investigations at fine-scales can clarify the interactions between seabirds and fisheries (Torres et al. 2013, Tew Kai et al. 2013), as well as provide insight into predator-prey interactions. Fine-scale hydro-acoustic surveys around penguin island colonies allow for the exploration of relationships between penguin behaviour, reproduction parameters and local fish abundance. From 2010 to 2013, Robben Island had a purse-seine closure area around the island. The closure provided an opportunity to look into the dynamics at play in the vicinity of the island without the complicating factor of purse-seine fishing. The benefits of purse-seine fisheries closures around Robben Island to African Penguins is under investigation (Cherry 2014). There is evidence chick survival improved during this period (Sherley et al. 2015).

Simulation models find the Robben Island colony population to be strongly driven by food availability using catches and large-scale pelagic fish biomass survey data (Weller et al. 2014). The fine-scale hydro-acoustic surveys present an opportunity to investigate whether chick body condition in the colony is explained by the local abundance of pelagic fish around the island. African Penguin chick mass increases linearly with the mass of food brought back to the nest by adults and the amount brought to chicks increases with chick size (Wilson et al. 1989). It seems logical that with greater fish abundance, fish will be more available to African Penguins provisioning chicks and thus that chicks will be better fed when prey is in greater abundance near the colony. It is possible that with a greater biomass of prey around the island, the provisioning distance at sea and prey capture time could be minimised allowing for more frequent feeds. Yet, the parents would still be limited by their stomach capacities and the return journey to their nest on land. So at some point there would be biological limits to the quantity and rate at which chicks can be fed by their parents in the wild.

The chick Body Condition Index (BCI) is for African Penguin chicks with head lengths above 75 mm (Lubbe et al. 2014). However, as efforts had been made to restrict device deployments to adults provisioning for small downy chicks at the P1/P2 stage (Chapter 4), most of the chicks in the foraging study had head lengths of < 75 mm and thus smaller than the Lubbe et al. (2014) BCI allows for. It is restricted to those larger head lengths because it relies on the linear relationship between chick head lengths of < 75 mm and body mass (Lubbe et al. 2014). A non linear extension is required for small chick sizes. An extended chick BCI would allow for an investigation into whether chick body condition at small sizes is linked to the body condition of their parents, and the foraging behaviour of a parent.

Anchovy is dominant in the diet of breeding African Penguins (Wilson 1985, Crawford et al. 2011, Sherley et al. 2013). Diet sampling at Robben Island from 1989 to 2009 found Anchovy contributed to > 55% of the prey percent mass (Crawford et al. 2011). Sherley et al. (2013) found 2- chick broods had higher fledging rates from 2001 to 2009 at Robben Island when Anchovy contributed to > 75% of the diet. Therefore, I hypothesize that colony chick body condition will increase with larger proportions of Anchovy in the diet and when there is higher abundance of pelagic fish within the 20 km radius of the island. Hydro-acoustic surveys for pelagic fish abundance at this fine-scale were conducted around Robben Island since 2010 by the Department of Agriculture, Forestry and Fisheries during the penguin breeding season, allowing for the investigation of the prediction that chick body condition at the Robben Island colony is better when local prey abundance and preferred prey type are in greater abundance.

The true relationship between pelagic fish abundance and colony chick body condition is likely to be curvilinear (Cairns 1988, Piatt et al. 2007). However, the range of fish abundance values of hydro-acoustics collected so far are unlikely to encapsulate the entire range of pelagic fish abundance especially considering the variability of the Southern Benguela, which is considered to have wasp-waste controlled ecosystem dynamics where there is both top down and bottom up control on the pelagic fish and their zooplankton prey (Cury and Shannon 2004). Therefore, I predict that responses will be linear, as was the case of food density comparisons with chick-feeding rates in Common Murres (*Uria aalge*) (Harding et al. 2007). Furthermore, in years of high food availability I would predict more birds would attempt to breed in the colony, such as inexperienced and inefficient foragers, and fledge chicks that would subsequently suffer higher mortality (Williams and Croxall 1990). For this reason we would be unlikely to observe a plateau in chick body condition so a linear approach investigation is appropriate.

This chapter extends the chick BCI to small chicks and explores whether African Penguin chick body condition is explained by the body condition of its parents or the foraging efforts measures of one of its parents. The chapter investigates whether chick body condition in the colony was related to the following extrinsic factors: the body condition of a parent, local pelagic fish abundance around the island and the proportion of Anchovy in the diet.

Methods

Ethics

All data collection was carried out under permit from the South African Government, Department of Environmental Affairs (DEA) and with the permission of the Robben Island Museum. All techniques were approved by the University of Cape Town Science Faculty Animal Ethics Committee or the Department of Environmental Affairs Animal Ethics Committee.

Data collection

Foraging data were collected at the Robben Island colony from 2011 to 2013, when a purse-seine fishing exclusion zone was in place out to a 20 km radius of the island. One breeding adult penguin of a pair provisioning small chicks at a nest was equipped with a Global Positioning System and temperature depth device for one foraging trip (Chapter 4). The bill length and bill depth of adults were measured with callipers to the nearest 0.1 mm. Both parents were weighed to at least the nearest 10 g with Rapala^{TM} hand-held scales and a harness (details provided in Chapter 4). Chicks were measured in cloth bags also to the nearest 10 g. Chick head lengths, from the tip of the bill to the back of the skull, were measured using callipers to the nearest 0.1 mm (Chapter 4).

Long-term monitoring of chick body condition has been undertaken at the Robben Island colony since 2008. Chicks were measured, as described above, at various colony locations weekly generally in two out of the four weeks each month from March to August and in some years monitoring continued into November. Efforts were made to sample different areas in the colony equally over each year.

Fine-scale hydro-acoustic surveys were conducted by the Department of Agriculture, Forestry and Fisheries (DAFF), Fisheries Branch, within a 20 km radius of Robben Island following a transect which curved laterally around the island as often as weather conditions would allow during the penguin breeding seasons from 2010 to 2014. The surveys were conducted from an inflatable boat with a standard 38 Hz scientific pole-mounted transducer and console-housed GPT (Merkle et al. 2009, 2012a, 2012b). At the time of writing, survey results were only available up to 2013. The pelagic fish abundance within a 20 km radius of the island was estimated from the survey data by DAFF following methods described in Jolly and Hampton (1990) and Coetzee et al. (2008) (Chapter 5).

Diet sampling has been conducted by DEA, Oceans and Coasts Branch, at Robben Island since 1989 (Crawford et al. 2011). Adult birds in transit back to their nests in the evening were sampled using the water-offloading technique (Wilson 1984). From each bird from which a diet sample is obtained, prey species were identified and weighed to obtain percent mass of different prey species (following Crawford et al. 2011).

Analysis

Extending the chick Body Condition Index (BCI)

The Lubbe et al. (2014) Body Condition Index (BCI) (eqn 3.1) was calculated for all chicks that had head lengths of > 75 mm. The predicted body masses were derived from the multiple measurements of 125 chicks that fledged successfully on Robben Island which were sampled in 2004 (Bouwhuis et al. 2007, Lubbe et al. 2014).The chick BCI uses quantile regression to compare a chick's mass with that of other chicks with the same head length. If the BCI value is > 1 the chick is in better body condition than the 95% quantile of those 2004 chicks while a negative BCI indicates the a chick in body condition was worse than the 5% quantile of the chicks that fledged successfully in 2004 (Lubbe et al. 2014).

A non linear quantiles were used to derive a BCI for Damara Tern (*Sterna balaenarum*) chicks using weighted regression methods (Braby 2011). This approach was followed to make the BCI applicable to African Penguin chicks with head lengths ≤ 75 mm. A weighted regression in GenStat (VSN International 2011) by Les Underhill was fitted for each 0.1 mm of chick head length (840 weighted quantile regressions) for the data set of the multiple measurements of 125 chicks that fledged in 2004. This gave the predicted chick mass at non-linear 5% and 95% quantiles for each chick head length from 38.0 mm to 122.0 mm by 0.1 mm for the entire data set (Supplementary Materials, Table S2.1). I used the 'INDEX' and 'MATCH' functions in Excel (Microsoft 2007) to identify the non-linear quantile mass values to calculate the extended BCI value for each chick measured at a nest during chick body condition monitoring from 2010 to 2014 and the foraging study from 2011 to 2013. For the Robben Island chicks that had head lengths > 75 mm and < 122 mm, both the Lubbe et al. (2014) BCI and the extended BCI presented were calculated and tested for a correlation between the two indices. The predicted range in body mass for chicks of different head lengths was examined using the range in body mass values from the 5% and 95% quantile values generated for chick head lengths of 38 mm to 122 mm.

Comparison of chick body condition to their parent's body condition and behaviour

Data exploration was conducted to look for relationships between the body condition of chicks and that of their parents using the measurements collected during the foraging research. I computed the adult BCI (Chapter 3) for the parents and the extended chick BCI for all chicks. The adult BCI values of pairs were plotted against each other to see if paired birds were in similar body condition. I compared the chick BCI values to the BCI values of their parents by plotting them against each other. To investigate whether parental foraging effort is linked to the body condition of their chicks, the individual chick BCI values were plotted against the foraging effort parameters of their parent equipped with a device with chicks that had been measured at deployment and then chicks that had been measured within three days of the parent's at sea foraging trip.

Colony chick body condition in relation to prey composition and abundance

To test for a relationship between chick body condition at the colony and the local pelagic fish abundance I used the total estimates of pelagic fish around the island from the hydro-acoustic surveys around the island, provided by DAFF (Chapter 5), and the chick measurements taken within 14 days of each survey. The colony chick BCI when sampled at 5-day sampling intervals gave similarly reliable results (Waller 2011). The 5-day sampling interval is in use for monitoring chick body condition at African Penguin colonies; however, for colonies that cannot be sampled as frequently, a two-week interval was deemed sufficient for estimating colony chick body condition (Waller 2011). Therefore, I used two weeks as the maximum sampling window to compare colony chick body condition to the local pelagic fish biomass around Robben Island. Shorter temporal windows of seven days and three days were also explored to see if this changed the strength or nature of the relationship with pelagic fish biomass.

I modelled the relationship between local pelagic fish biomass in thousand tonnes (10^3 t) around the island and chick body condition as well as the relationship between prey mass composition in the adult diet samples using linear-mixed-effects models. I hypothesized that both percentage of Anchovy in the diet as well as overall pelagic fish abundance around the island would influence chick body condition The relationships would be positive. However, all three data data sets were seldom collected simultaneously (only 3 months) and for this reason these explanatory variables were modelled separately. The modelling was performed using the 'lme' function in the Nonlinear Mixed-Effects Models 'nlme' package (Pinheiro et al. 2014) in the R statistical environment (R Core Team 2013) following a top down strategy (Zuur et al. 2009). To account for any correlations in the data with time of sampling that could be due to weather or environmental conditions at the time of the survey or sampling, I investigated which random effects best explained the random variation in the data: year, month nested in year, survey, and survey nested in year. The AIC values of the different random effects models were compared using restricted maximum likelihood (REML). Then, as there was only one fixed effect of interest in the models, the model was rerun with the random effects that best explained the random variation in the data with REML fitting to report the model coefficients. There were a large number of gaps or NA values in the diet data and fine-scale survey data, so 'NA remove' was part of the statisitcal model. Where significant results were found the model coefficients from the REML output were reported and plots were generated of the linear mixed-effects model, using the allEffects function in the 'effects' R package (Fox et al. 2014). Plots of the model residuals were examined to check the assumptions of residual normality and homogeneity of variance were met.

Results

The chicks of equipped penguins mostly had head lengths < 75 mm and when compared with those 125 chicks that fledged successfully measured in 2004, the relationship with body mass was non-linear in these chicks (Fig. 6.1A). The BCI extension produced the 95% quantile (maximum predicted mass) and the 5% quantile (minimum predicted body mass) for chick head lengths ranging from 38.0 to 122.0 mm (Fig. 6.1B). The body mass values at these quantiles are provided in the supplementary materials S2 (Table S2.1). The predicted range in body mass between the 95% and 5% quantiles increased with chick head length (Fig. 6.2). The Lubbe et al. (2014) BCI and the extended BCI were calculated for 1,788 chicks with head lengths from < 75 to 122 mm; they were highly correlated (r = 0.99, t_{1786} = 441.6, p < 0.001, Fig. 6.3).

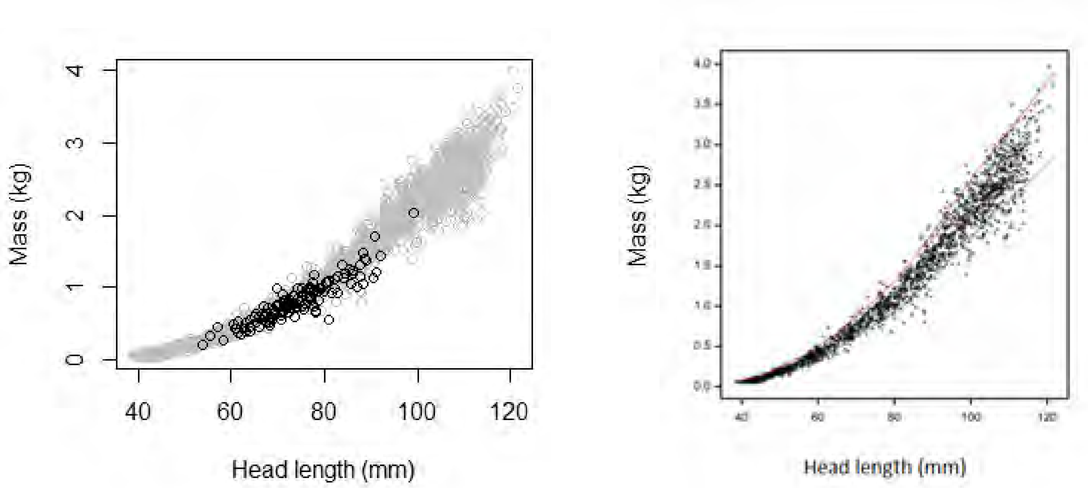

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Figure 6.1. Plots of Robben Island colony African Penguin chick body mass as explained by head length for (A) 132 chicks of equipped birds measured once from 2011 to 2013 (in black) over the multiple measurements (in total 1,926) from 125 chicks that fledged successfully in 2004, collected as part of an energetic study (Bouwhuis et al. 2007) shown in grey. (B) the smoothed non linear 95% quantile in red and 5% quantile in green for the 2004 measurements.

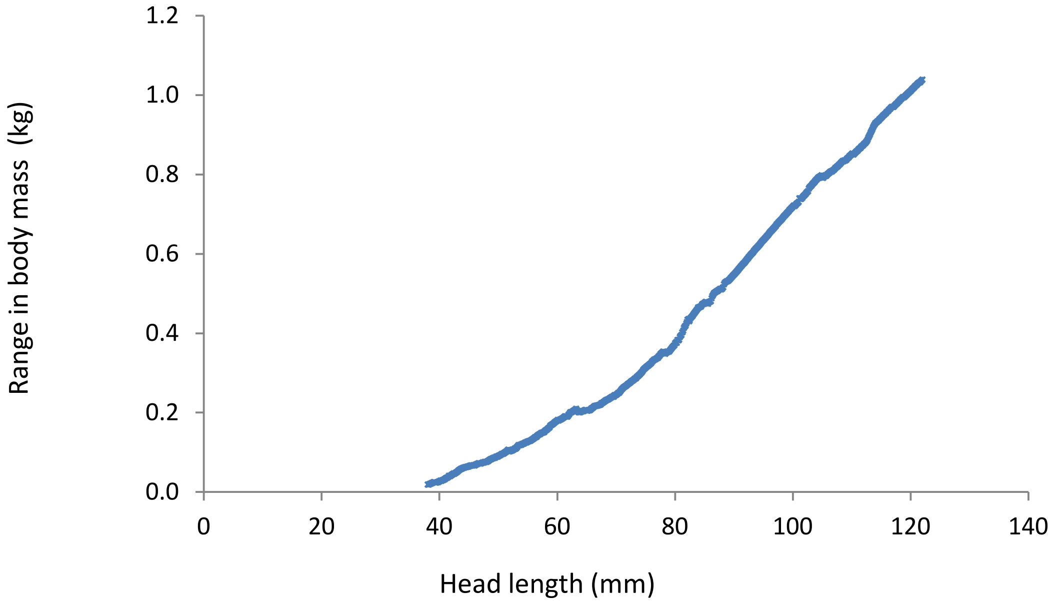

Figure 6.2. The predicted range in African Penguin chick body mass for chicks of head length 38 to 122 mm, calculated from the 95% and 5% non-linear quantiles for the 2004 data set of multiple measurements of 125 chicks that fledged successfully. There is an increase in the body mass range of chicks of larger sizes and hence greater possible variation in body condition as chicks grow larger.

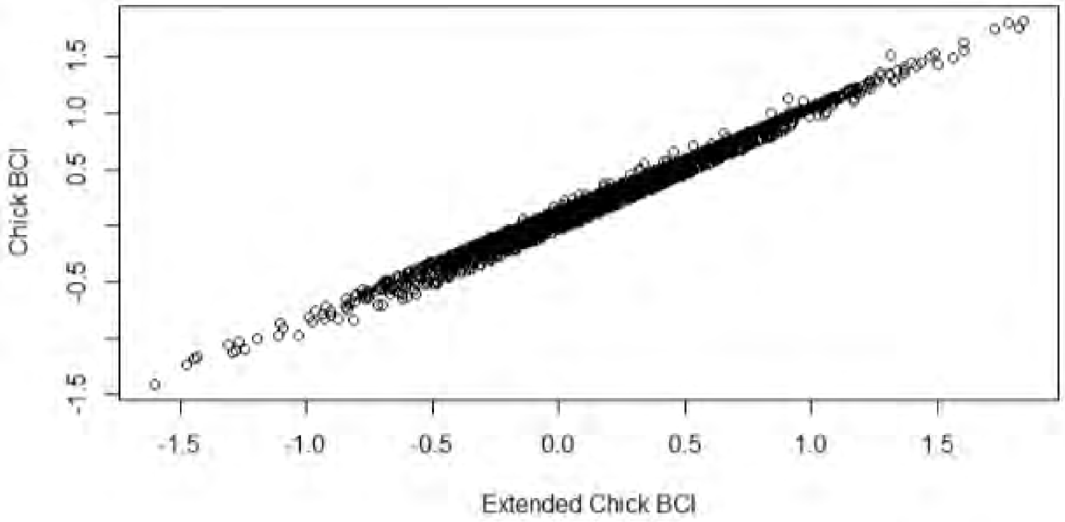

Figure 6.3. The scatter plot of the two African Penguin chick Body Condition Indices (BCI) showing the high correlation between the original BCI by Lubbe et al (2014) and the extended version for 1,788 chicks with head length within 75 and 122 mm.

A total of 132 chicks were measured during the foraging research on Robben Island from 2011 to 2013. In most cases both parents were in good body condition but in five cases one of the parents was in poor body condition while the other was in good body condition and in one case both birds of a pair were in poor body condition (Fig. 6.4). Using the extended chick BCI, I investigated whether chick body condition was explained by the body condition of their parents or the foraging efforts of one of their parents. As the number of days between the time the parent was at sea with a device and the day chicks were measured was on average 2.2 days (range: −1 to 10 days) I restricted analysis to chicks that had been measured < three days from the day the parent was at sea. I assumed the change in chick body condition over two days or less to be small enough to be negligible and examining shorter and longer temporal windows did not change the patterns observed. Plots of chick and their parental body condition showed no relationship (Fig. 6.5). There were no significant correlations. I also looked at B chicks separately and singletons separately and there was no relationship. Neither was the parent with the lower BCI related to the BCI of their chicks. There was no relationship between the chick body condition and the equipped parent's foraging behaviour (Fig. 6.5). This indicates that one foraging trip is unlikely to solely indicate the body condition of a bird's chicks because it is likely dependent on multiple feeds by both parents, diet and environmental effects.

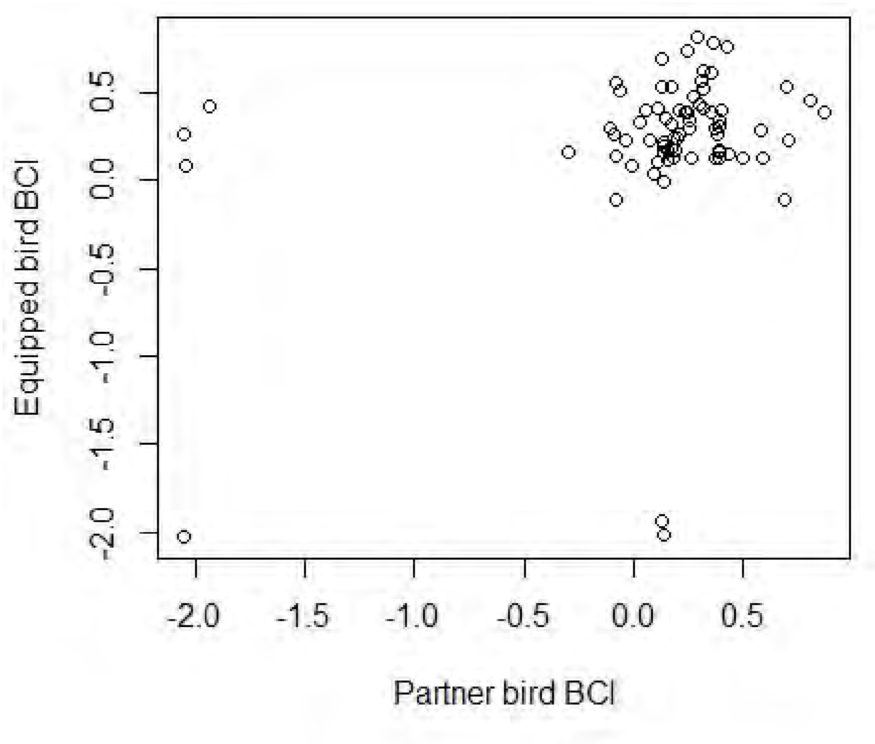

Figure 6.4. African Penguin Body Condition Index (BCI) of 124 breeding pairs for which both the equipped penguin and partner were measured.

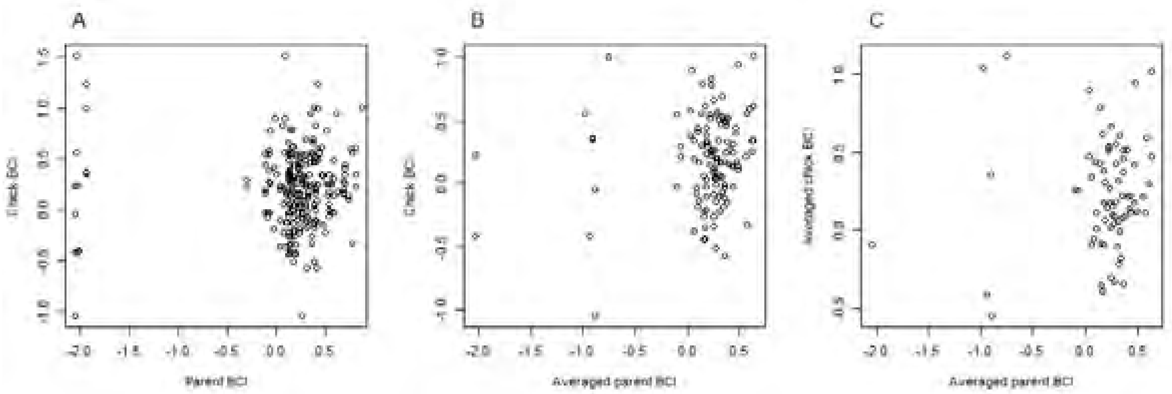

Figure 6.5. African Penguin Body Condition Index (BCI) of 123 small chicks against the body condition of their parents (78 pairs) at Robben Island for (A) the body condition of all individuals, (B) the chick BCI against the averaged parent BCI and (C) the averaged chick BCI against the averaged parent BCI. The measurements were pooled from three breeding seasons from 2011 to 2013 but individuals were only measured once.

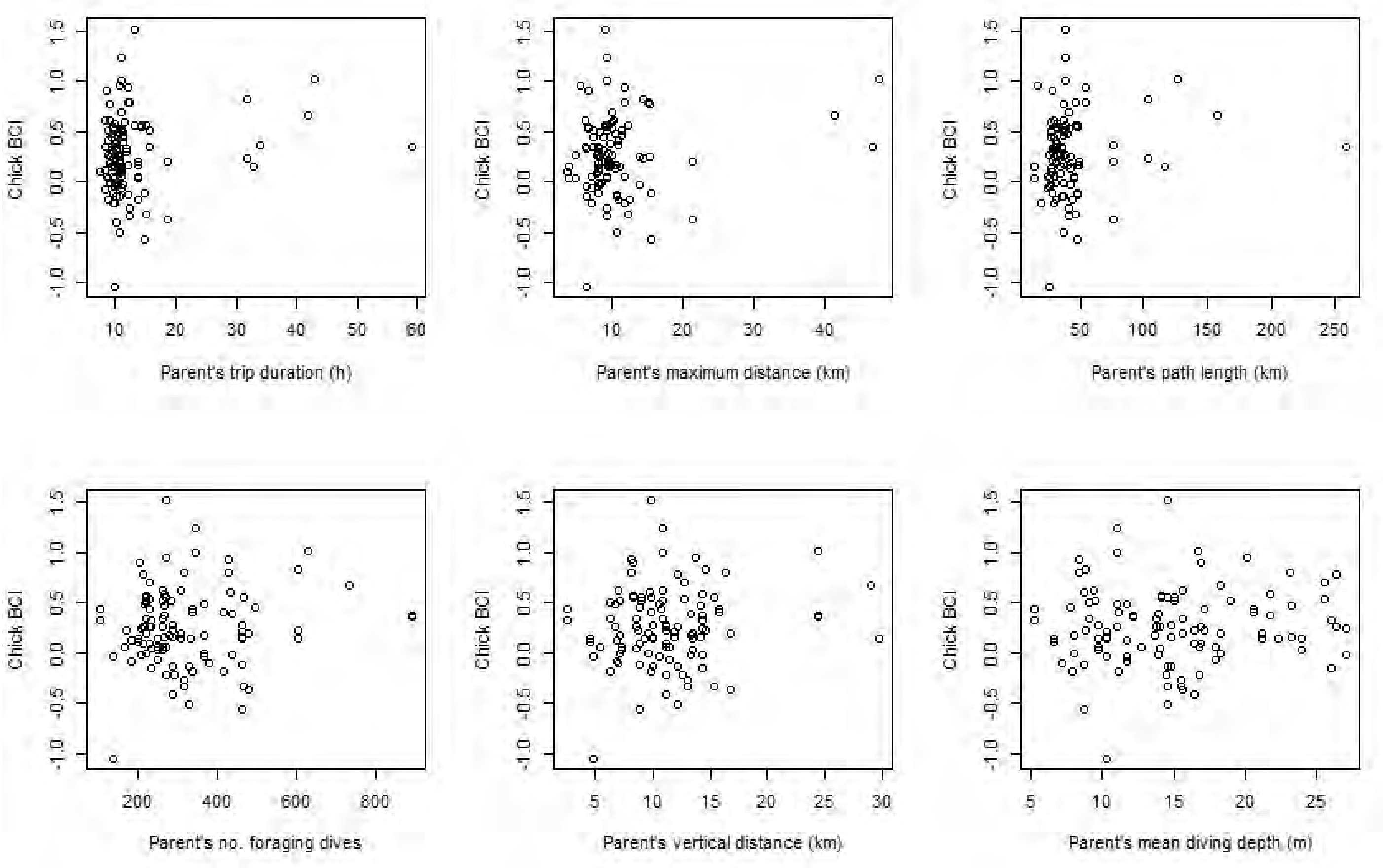

Figure 6.6. African Penguin chick Body Condition Index (BCI) against foraging measures of a parent at sea within three days of the chick's measurements. See Table 4.2 for foraging measure definitions.

Robben Island chick BCI in relation to pelagic fish abundance around the island from 2010 to 2013 was investigated at three different temporal windows: within three, seven and 14 days of surveys. In all cases survey best explained the random variation in the data. At the three and seven day temporal windows the biomass showed positive relationships with chick body condition but these models were not significant ($p > 0.05$). The three-day temporal window only allowed for 260 chick measurements to be compared with six hydro-acoustic surveys and chick measurement sample sizes per fish survey were small with a mean of 34 chicks (range: 3 to 105). While the seven-day window allowed for 503 chick measurements to be compared with 12 hydro-acoustic surveys, the numbers of chicks measured per fish survey were still low with a mean sample size of 42 chicks per fish survey (range: 3 to 105). Chick body condition within 14 days of a fine-scale survey allowed for the comparison of 13 fine-scale surveys with 801 chick body condition measurements and on average 61 chicks per fish survey (range: 9 to 113). At this temporal window, chick body condition significantly increased with the abundance of local pelagic fish biomass around the island (Table 6.1). The model predicts for an increase in 10×10^3 t of pelagic fish biomass in the area out to 20 km around Robben Island the chick BCI in the colony increases by a magnitude of 0.02. It predicts an increase in colony chick body condition of 245% could be expected over the range of fish abundance of 186.5×10^3 t observed, from 0.5×10^3 t to 187×10^3 t (Fig. 6.7). Thus, with higher pelagic fish abundance around the island chicks attained better mass for their structural size. Examining the normal Q-Q plot of the residuals and the standardized versus fitted residuals showed the assumptions of the model had been met (Fig. 6.8).

Table 6.1. Mixed effects model results of Chick Body Condition Index (BCI) as explained by the fixed effect of abundance of pelagic fish biomass (103 t) around 20 km radius of Robben Island as identified by fine-scale hydro-acoustic surveys with survey as the random effect.

Model parameter	Value	Standard error	df	*t*	p-value
Intercept	0.151	0.058	788	2.58	0.01
Slope	0.002	0.001	11	2.54	0.03

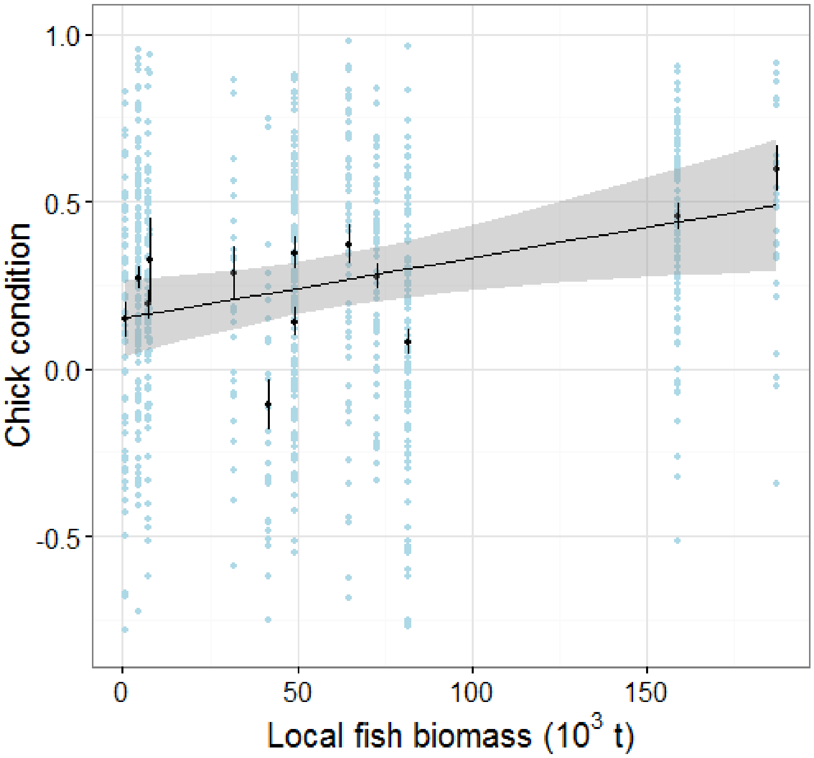

Figure 6.7. African Penguin chick body condition (N = 801) at Robben Island as explained by pelagic fish biomass abundance in a 20 km radius around Robben Island, from 13 hydro-acoustic surveys over 2010 to 2013. The black line shows the linear mixed effects model with the 95% confidence intervals in grey. The actual chick body condition mean ± SE is plotted as points on top of the effects plot for each fish survey. Chick body condition was calculated with the extended body condition index to incorporate all available chick measurements taken within 14 days of a fish survey around the colony.

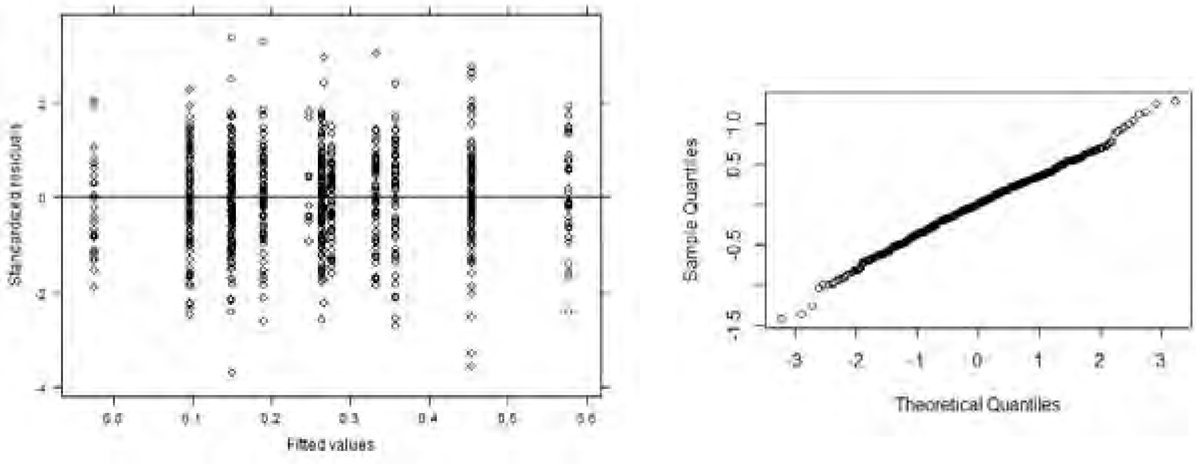

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Figure 6.8. Model diagnostics for the linear mixed-effects model of the Robben Island colony chick Body Condition Index (BCI) extended version as explained by the pelagic fish abundance around 20 km of Robben Island: (A) the standardized residuals and fitted values of the linear mixed effects model of chick body condition and (B) the Q-Q normality plot of the model residuals show no violations of model assumptions. In this case, the temporal window examined was chick measurements within 14 days of a hydro-acoustic survey around the island.

There were 42 months between 2008 and 2013 for which chick body condition data were available, and of those 24 months for which both chick body condition and diet sampling were conducted. The extended chick BCI was calculated for 2,220 chicks with head lengths up to 122 mm. These were examined in relation to the proportion of Anchovy in the diet for those months using the linear mixed effects modelling. Month in year best explained the random variation in the chick body condition data. There is evidence for a positive relationship between the percentage of Anchovy in the diet and chick body condition, the slope coefficient ± SE was estimated at 0.003 ± 0.001 ($p = 0.05$). There is a 5% probability this result was by chance so further investigation with a larger number of diet sample months is recommended. This model indicated chicks are in better body condition when Anchovy made up a larger proportion of their diet (Fig. 6.9). The model diagnostics showed the assumptions of the residuals in the model had been met (Fig. 6.10).

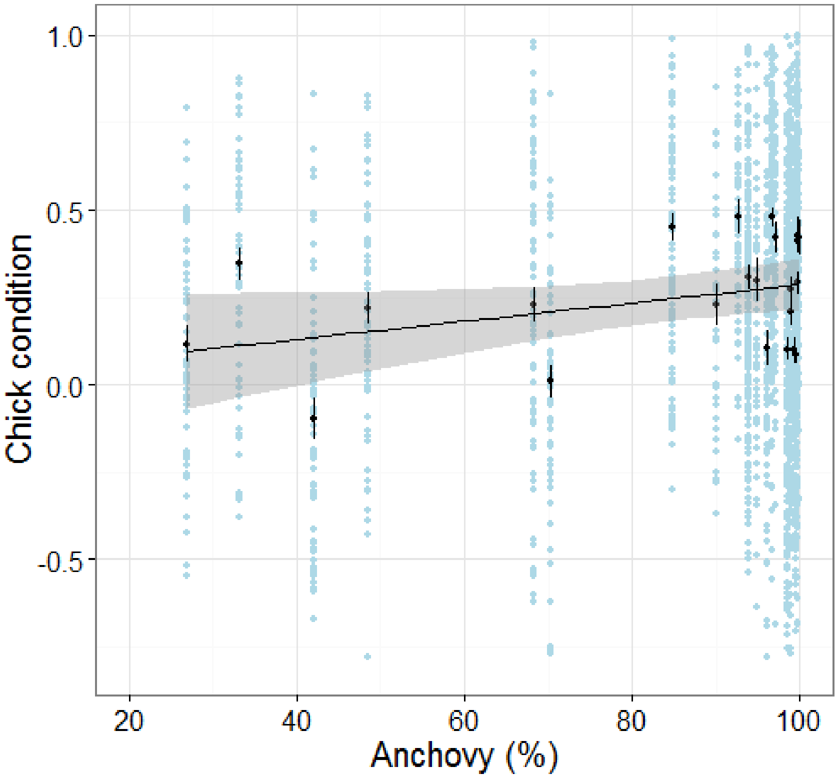

Figure 6.9. Body Condition Index (BCI) of 2,220 African Penguin chicks as explained by the percentage of Anchovy in the diet of adults in transit back to their nests, sampled over 23 months from 2008 to 2013 in light blue. The linear mixed effect model with month nested in year as the random effect is shown as the black line with 95% confidence intervals in grey. The chick body condition mean ± SE at each month that diet was also sampled on top of the effects plot in black points. There were only 6 months were the percentage of Anchovy in the diet was < 80%. For this reason, there is more uncertainty in the confidence intervals around the lower Anchovy percentages.

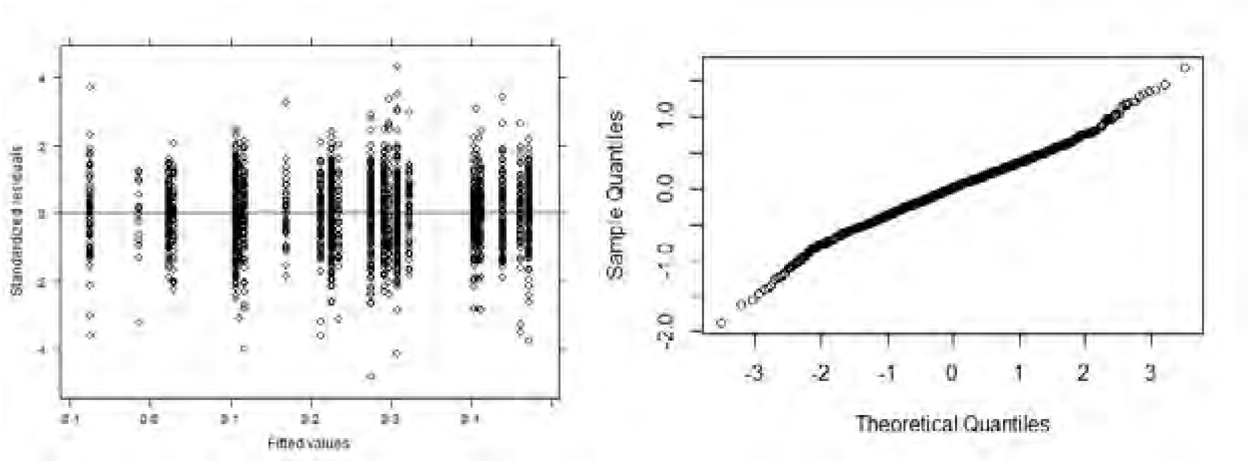

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Figure 6.10. Model diagnostics for (A) the standardized versus fitted residuals normal and (B) the normal Q-Q plot of the residuals for the linear mixed-effects model of African Penguin chick body condition (BCI) extended as explained by the percentage of Anchovy in the diet that month, with month nested in year as the random effect.

Discussion

The extended chick BCI presented provides a measure of body condition for chicks with head lengths < 75 mm. The Lubbe et al. (2014) chick BCI has been extended past the range of data for which it was created. Extrapolations of regression models beyond the dataset with which they were parameterised should be treated with caution (Zar 2010). The extended chick BCI is appropriate for chick head lengths from 38.0 mm to 122.0 mm. Even though chicks may grow at a slower rate when small (Cooper 1977) they can still vary in body condition; however, the range of body mass for their structural size increased with head length (Fig. 6.3). This corresponds to the finding that large chicks, at c. 90 mm to 105 mm head lengths, have the highest daily energetic requirements (Bouwhuis et al. 2007). Thus, measurements of chicks with larger head lengths are more likely to give meaningful indications of chick body condition . I recommend that data collection remains focused on chicks with head lengths > 75 mm to maintain consistency in methodology and to minimize disturbance at nests with small chicks. The two indices are highly correlated at these head length sizes as would be expected. The extended chick BCI allowed the calculation of chick body condition for small chicks in this study.

There was no relationship found between chick body condition and the measures of one parent's foraging behaviour (Fig. 6.5). One foraging trip from a parent is a brief snap shot of parental activity and provisioning behaviour and may not provide enough of a signal for it to be distinguished in chick body condition. Considering deployments were restricted to adults with small chicks, which tend to have lower energy requirements (Bouwhuis et al. 2007) and the potential for differences in body condition is relatively low it appears that a relationship, should one exists is not detectable at these chick sizes. It could be that a relationship might be identified if the provisioning behaviour of both parents were to be examined over multiple feeds. In other seabird species, relationships have been identified between parental body condition and the amount of food delivered to chicks (Tveraa et al. 1998, Ballard et al. 2010). This requires further investigation in the African Penguin.

In the near-shore foraging Little Penguin (*Eudyptula minor*) provisioning behaviour is related to chick fledging weights (Chiaradia and Nisbet 2006, Saraux et al. 2011). Little Penguins alternated longer trips when their body mass was low with short trips for provisioning during chick rearing; birds that had an increase in the proportion of long trips decreased fledging success and chick fledging weights (Saraux et al. 2011). African Penguin foraging trip durations were highly skewed to the right but they were not bimodal (Fig. 4.8). Peak chick weights are negatively related to mean foraging trip durations of both parents in Little Penguins (Chiaradia and Nisbet 2006). Thus, it is possible the behaviour of both parents and multiple trips would indicate the body condition of chicks.

Data from multiple foraging trips would probably be needed to detect whether such plasticity in foraging behaviour exists in the African Penguin. Automatic penguin monitoring systems (APMS), make it possible to investigate relations using multiple provisioning trips (Ballard et al. 2010, Saraux et al. 2011). The application of an APMS to investigate foraging trip durations would be complicated at an African Penguin colony like Robben Island where there are multiple routes penguins take to the sea (Sherley et al. 2010).

The results of this chapter indicate African Penguin chick provisioning is influenced by both local prey abundance and quality. Anchovy has an energy content of 6.03 kJ/g (Balmelli and Wickens 1994), which is high relative to most other items commonly found in the diet of African Penguins at Robben Island (Sherley et al. 2013). This is likely the reason for a preference for Anchovy when available in the diet of African Penguins (Ludynia et al. 2010). These results confirm predictions that chicks raised on a diet with more Anchovy, a high energy content fish, were in better body condition (Table 6.2, Fig. 6.9). It is known from experimental evidence that poor nutritional diets can retard African Penguin growth rates (Cooper 1977), chick feather development and cause starvation (van Heezik and Seddon 1992). However, as Cairns (1988) pointed out, chick growth can be impacted by other influences such as weather conditions, and so can chick body condition. Exposure and nest flooding can cause African Penguin chick mortality (Seddon & van Heezik 1991). Nevertheless, this chapter shows African Penguin chick body condition is positively related to pelagic fish abundance around Robben Island (Table 6.1, Fig. 6.7). The finding is similar to the non-linear relationships between prey density and chick body condition at fledging in Common Murres and Black-legged Kittiwakes (*Rissa tridactyla*) (Piatt et al. 2007). Further investigation with a larger range of prey densities around the island is recommended to confirm the functional nature of the positive relationship for African Penguin chick body condition to local pelagic fish abundance.

This chapter provides further evidence of the sensitivity of African Penguin penguins, as central place foragers when breeding, to the pelagic fish abundance in the local area of their colony (Petersen et al. 2006, Durant et al. 2010, Sherley et al. 2013). Chick body condition increased with prey abundance within the 20 km radius of the colony and with higher proportions of Anchovy percentage in the diet. These findings provide possible mechanistic explanations for the increased chick survival during purse-seine closure years (Sherley et al. 2015). Minimising human fishing pressure in the vicinity of penguin colonies could prevent depleting the abundance and percentage of Anchovy recruits moving through the area. While no-take zones can benefit African Penguins in terms of decreasing foraging effort and increasing chick survival (Pichegru et al. 2010, Sherley et al. 2015), if fishing increases at the boundaries of these zones the benefits expected may not be observed (Pichegru et al. 2012). On the other hand, if closure zones increase the local fish abundance around island colonies or Anchovy composition in the diet then the results indicate this would be beneficial to African Penguin reproduction.

Conclusions

The chapter found that chick body condition was related to local prey abundance and composition. The results indicate chick body condition decreases when pelagic fish are locally less abundant and when there is a lower percentage of Anchovy in the diet. Local prey resources are influential factors on chick provisioning. This has implications for fisheries closure zones and needs to be taken into consideration in spatial fisheries management and African Penguin conservation.

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Chapter 7

African Penguin chick survival in relation to parental provisioning and human disturbance from foraging research: can foraging distance be a leading indicator of breeding success?

Behaviours related to demographic processes and environmental conditions can be used as indicators of when conservation efforts are needed. A leading indicator of breeding success (i.e. an indicator that precedes the breeding outcome) would be useful for conservation efforts of imperiled African Penguins (*Spheniscus demersus*). It could help identify times when conservation efforts such as chick bolstering are needed to improve chick survival. In this chapter, foraging behaviour was examined in relation to breeding success and reproductive output to see if it could be a leading indicator. Sampling of foraging behaviour of breeding African Penguins with GPS temperature devices was restricted to one foraging trip because of the species 'Endangered' IUCN status. Breeding success monitoring was conducted for the nests in the foraging study as well as a control sample in the colony. Survival analysis was conducted using Mayfield methods. Chicks in the foraging study had the same survival as the control chicks. At the scale of a foraging trip from one parent, foraging effort did not explain chick survival. However, penguins that had unsuccessful breeding success travelled further from the colony than penguins that had nest failures. Chick survival was comparable between years so further investigation is needed with dissimilar years to identify whether foraging distance could be a leading indicator of African Penguin breeding success at a colony.

Introduction

Behaviours can be used as indicators of patterns of population change which can be useful for conservation efforts (Morris et al. 2009). Identification of leading indicators for breeding success would be particularly useful for endangered species like the African Penguin to assist with the determination of when conservation interventions are needed. An indicator of poor reproductive conditions prior to nest failures would be useful for conservation initiatives such as chick bolstering interventions in which chicks are being hand-raised in captivity after nest abandonments and released; successfully contributing to African Penguin population growth (Sherley et al. 2014b). Determining if foraging distance could be used as an appropriate leading indicator of reproductive conditions requires examining the relations between parental provisioning and chick survival. The impact of the disturbance from foraging research needs to be considered to identify whether survival probabilities of chicks in the foraging study are comparable to chicks monitored in the colony for breeding success.

African Penguins are range-restricted central-place foragers when breeding (Ryan et al. 2004), with chicks reliant on parental provisioning until they fledge at between 55 and 130 days old (Crawford et al. 2013). African Penguin provisioning behaviour is used as an indicator of feeding conditions (Petersen et al. 2006). In the closely related Magellanic Penguin (*S. magellanicus*) (Ksepka et al. 2006), the average foraging distance affects reproductive success (Boersma and Rebstock 2009) and foraging distance differs between successful and unsuccessful breeding attempts (Boersma et al. 2015). Accordingly, African Penguin foraging effort should be expected to correlate with reproductive success. However, the African Penguin currently has an 'Endangered' species' status (BirdLife International 2013). Precautionary measures limit the foraging research conducted on the species during breeding. Study birds are generally only equipped with a GPS tracking device once for one foraging trip. Thus, whether African Penguin foraging behaviour can be a leading indicator for reproductive success at a nest or colony level, given the restricted sampling, is unclear but has implications for species monitoring. Studies on the effects of equipping breeding African Penguins with logging devices have been largely focused on the birds themselves with little to no empirical investigation on impacts on their chicks (Wilson and Bain 1984a, 1984b, Wilson et al. 1986, Petersen et al. 2006, Pichegru et al. 2010). Equipping African Penguins with devices that are larger than 6.8% of a penguin's cross-sectional area can cause a deficit in energy provided to chicks (Wilson et al. 1986). If there is a device effect on the food delivery amount it is likely to be limited to one feed but whether that and disturbance from investigator(s) results in a cost to breeding success needs to be examined.

Nest checks in penguin colonies can impact chick survival (Giese 1996). The human disturbance involved in nest checks — entering a colony and lifting birds to check nest contents as opposed to observation from a distance — reduces chick survival in Adélie Penguin (*Pygoscelis adeliae*) colonies (Giese 1996). In the African Penguin, nest monitoring cannot be done from a distance, particularly at the Robben Island colony where most nest contents are hidden under vegetation, in burrows, or under man-made objects (Sherley et al. 2012a). In addition, the vegetation and distribution of nests on the island do not allow for a clear vantage point for colony observations (Sherley et al. 2014a). It is possible to compare the increased disturbance to nests in the foraging study with the other nests monitored on the island. In this way, examining whether the added disturbances involved in equipping the logger, frequent nest checking and chick and parent handling for measurements impacts chick survival more than the regular nest checking conducted for breeding success where no handling occurs. The current monitoring of African Penguin breeding success has taken place at Robben Island since 2001 (Crawford et al. 2006, Sherley et al. 2012a). It allows for a comparison of survival probabilities between chicks involved in foraging research and the chicks being monitored for breeding success in the colony (the control group).

This chapter investigates the relationship between parental provisioning behaviour and chick survival in the African Penguin. I tested whether chicks involved in the foraging study had comparable survival probability to the control group. Subsequently, I examined whether the variation in chick survival can be explained in part by the foraging behaviour measures of one trip of one parent. Lastly, I explored the foraging distance of penguins provisioning chicks and their subsequent breeding attempt and reproductive success to examine its potential as a leading indicator. Considering previous findings (Giese 1996, Boersma and Rebstock 2009), I hypothesised that: (1) foraging study nests will have lower fledging success than nests monitored in the colony for breeding success because the foraging study involved more human disturbance; (2) lower foraging distances will be related to higher breeding success but that (3) on a per chick basis, foraging data collected will not indicate chick survival because it is only a small sample of the parental provisioning behaviour over the chick-rearing period.

Methods

Ethics

The research was conducted under the auspices of the Oceans and Coasts branch of the South African Department of Environmental Affairs (DEA). The penguin handling, techniques and monitoring had approval from DEA, the Robben Island Museum and the University of Cape Town's Science Faculty Animal Research Ethics Committee.

Data Collection

Data were collected at Robben Island, a protected UNESCO World Heritage Site and a west coast African Penguin colony in South Africa (Table Bay, 33°48'S, 18°22'E; Fig. 4.1), in 2011, 2012 and 2013. For the foraging research, nests were selected in which African Penguin adults were provisioning small chicks (one or two chick broods) and sharing parental care evenly – switching chick brooding on a daily basis. African Penguins breed in a variety of nest types on Robben Island (Table 1 of Sherley et al. 2012a). The most predominant nest type at the Robben Island colony are nests under vegetation (Sherley et al. 2012a). Penguins nesting in nest boxes were chosen over other nest types because these nest types reduced capture times and minimised the risk of the birds running away from the nest after release. Devices were not deployed on flipper banded penguins or those that showed signs of stress such as vocalisation or trembling during nest checks. GPS-TDlog devices were deployed on one of the parents for one foraging trip (Chapter 3). The foraging distance was calculated as a straight line distance from Robben Island to the furthest trip point (e.g. Boersma and Rebstock 2009). The trip duration, path length, and total time diving were calculated as defined in Table 3.2.

To compare chick survival between chicks in the foraging study and chicks monitored in the colony, nest visits were continued where possible to nest outcome by weekly nest checks (following Sherley et al. 2012a). On each visit, chicks were classified into stages of P0, P1, P2, P3 and P4 following Barham et al.(2007) (Fig. 1.5). Intervals between nest checks were mostly weekly from March to October but irregular intervals did occur, the minimum interval between checks being 4 days apart and the maximum being 20 days apart. Chicks were not marked so the larger chick was always assumed to be the A chick. The B chicks are more susceptible to death from starvation (Seddon and van Heezik 1991). When one of the chicks in a nest disappeared or failed it was assumed that it was the younger B chick. These assumptions were those used in previous African Penguin breeding success studies (Sherley 2010, Sherley et al. 2012a, 2013). In the case of abandonment after logger deployments chicks were removed to SANCCOB. Those chicks were not excluded from the analysis but treated as truncated observations. In the cases where deployments did not yield data no further measurements were taken at the nest and those nests were not followed to outcome.

Analysis

Chick survival

Following the Mayfield approach (Mayfield 1961, 1975) to account for the error in observational biases inherent in nest monitoring, I considered the number of chick nest days as units of exposure, calculated to the nearest half-day. The number of nest days a chick was observed for was calculated as the number of days between the midpoint of the penultimate visit and last visit the chick was observed minus the date the chick was estimated to have hatched or the first observation of chicks if there had been no prior visits (following Sherley 2010). Nests were added to the samples throughout the breeding season as in Barham et al. (2007), and Sherley et al.(2012a, 2013, 2014a). Extensions of this method have allowed for explanatory variables to be incorporated into the breeding success modelling (e.g. Kemper 2006, Pichegru 2012, Sherley et al. 2012a). I investigated chick survival probabilities during chick-rearing with explanatory factors.

Following Sherley et al. (2012a, 2012b), the maximum likelihood estimate of risk of failure per sampling interval (daily mortality rate), *F,* with one explanatory variable x, was defined as:

$$F = e^{(-\alpha-\beta x)} \qquad \text{(eqn. 7.1)}$$

where α is the intercept and β the coefficient. It can then be back transformed to get the nest survival, *S*, at time t as:

$$S(t) = e^{(-Ft)} \qquad \text{(eqn. 7.2)}$$

The 95% confidence intervals were then estimated as:

$$e^{\left(-tF-1.96\frac{F}{\sqrt{n}}\right)} \text{ and } e^{\left(-tF+1.96\frac{F}{\sqrt{n}}\right)} \qquad \text{(eqn. 7.3)}$$

The average fledging period for the African Penguin in the Western Cape is routinely estimated to be 74 days (e.g. Wolfaardt et al. 2008, Sherley et al. 2012a, 2013, 2014a). The fledging survival probabilities were calculated for the fledging period, t, of 74 days.

Parametric modelling of chick survival was conducted with an using the 'survreg' function in R (R Core Team 2013). The exponential error distributions are the most appropriate because this approach assumes that nest failure probability is constant and independent of time (Crawley 2007, Zador et al. 2009, Sherley et al. 2012a, 2012b). Analysis was done on a per chick basis, meaning the nest days were calculated for each chick separately (and not nest contents as a whole). The model uses the time to fail calculated in nest days. Chicks disappearing after less than 40 nest days counted as a failure. That is the earliest age at which chicks start to be left unguarded -the post-guard stage (Cooper 1977, Seddon and van Heezik 1993). If chicks were observed over 40 nest days and then were no longer observed it was assumed the time to failure was truncated as it was possible that chicks had joined crèches and time of mortality if it occurred was unknown. For chicks which fledged, mortality would have occurred after the end of the observation period, so the data were considered right censored.

In this way, I was able to see whether chick survival differed in the control nests between the years of the study. Then we can examine at whether the factor of being in a foraging study nest resulted in lower chick survival. Considering nest type is influential to chick survival (Seddon and van Heezik 1991, Pichegru 2012, Sherley et al. 2012a), I only used the most common nest type – under vegetation – for the comparisons. Year as a factor was examined first with the control nests under vegetation. Subsequently, years were combined to compare nests under vegetation in the foraging study with the control nests under vegetation.

Foraging behaviour of one parent's trip and chick survival

To examine chick survival as explained by foraging distance, trip duration, and path length all chicks in the foraging study were used. Years and nest types were combined as sample sizes would otherwise be too small. Each foraging effort variable was modelled separately because these variables are correlated (Table 3.5). The model AIC values were compared in R.

Foraging behaviour and breeding success

African Penguin chicks are typically considered to have fledged successfully if they were observed at the fifth stage of development, P4, when they obtained full juvenile plumage (Barham et al. 2007, Sherley et al. 2012a, 2013). They reach this stage generally at the age of 60 days old prior to leaving the nest (Seddon and van Heezik 1993). The foraging behaviour likely to indicate reproductive success is foraging distance (Boersma and Rebstock 2009). To investigate whether the foraging distance of one trip could indicate breeding attempt success, I compared the foraging distance of penguins that successfully fledged at least one chick to a possible fledging age (i.e. at the P4 stage) with the behaviour of penguins that had unsuccessful breeding attempts. Sample sizes were small so comparisons were conducted with box-plots, *t*-tests and permutation testing following Manly (1991) for differences of the means and inter-quartile ranges because permutation testing makes no assumptions about the underlying error distribution. The permutation tests consisted of first calculating the difference between the means (or the inter-quartile ranges) between the foraging distances of the two groups: successful and unsuccessful reproductive attempt outcome. To conduct the permutation test, the data of both groups were merged into one sample. Then random samples of the same group sizes as our original group sizes were taken without replacement and the difference between means (or inter-quartile range) computed. This was conducted 10 000 times in a loop in R. All the differences calculated were then sorted and compared with the original calculation to identify the significance level.

To examine foraging distance in relation to reproductive success of zero, one or two chicks fledged, only penguins with two chick broods at the time of deployment were included. The distributions were examined with box plots. Sample sizes were small so differences were assessed with ANOVA and then permutations across groups, calculating an *F* value each time. The original *F* value was then compared with the *F* values of the permutations to find the percentage of repetitions in which the values exceeded the original F value. This provides the p-value under the null hypothesis that an observation from one group could have as easily come from another group.

Results

The number of nests in the foraging study were 32, 42 and 16 in 2011, 2012 and 2013, respectively. Those nests had a total of 155 chicks observed but only 152 were alive at deployment. Devices had to be removed from three penguins prior to departure from the nest (in two cases the bird had stayed at the nest too long for the battery to last for a foraging trip and in one case because its chick had disappeared). The devices yielded complete data sets 83% of the time (72 out of 87 deployments). No devices were lost. Of the nests monitored in the colony, those which had flipper banded penguins with a known history of being oiled were excluded to prevent bias (Sherley 2010). This gave samples of: 141, 131 and 130 nests in 2011, 2012 and 2013, respectively. A total of 492 nests were monitored and 89% (440) were nests under vegetation (Table 7.1).

Table 7.1. The numbers of African Penguin chicks monitored and their nest types that were part of the foraging study with the rest of the colony in nest types under vegetation in 2011-2013.

Breeding success parameter	Foraging research group		Colony (control) group	
	All nest types	Nests under vegetation	All nest types	Nests under vegetation
Number of nests	90	67	402	373
Number of chicks	155	113	730	638
Number of failures	41	29	185	170
Failed (%)	26.5	25.7	25.3	26.6

Chick survival results

There were 751 chicks monitored that were in nests under vegetation. Excluding the nests that were in the foraging study, there were 217 chicks under vegetation monitored in 2011, 203 in 2012 and 218 in 2013. Chick survival probabilities did not differ between those years ($x^2 = 1.7$, p = 0.43; Fig. 7.1A). Subsequently, I combined the data for all years for nest types under vegetation to compare the survival of the chicks in the foraging study (N = 113) with the control group (N = 638). They showed a difference in survival probabilities of 0.01 which was not significantly different ($x^2 = 0.06$, p = 0.80; Fig. 7.1B). Chicks in the foraging study which had more frequent nest checks, human handling for measurements and a parent equipped with a device for a foraging trip had equivalent survival probabilities as those in control nests (Fig. 7.1B).

For all the chicks in the foraging study followed to outcome, I checked whether chick survival was explained by the foraging distance, trip duration, path length of the equipped parent's foraging trip but none of those explanatory variables explained the variation in chick survival (all p > 0.10). The AIC values did not differ from the null model by more than two so these factors did not explain the variation in the chick survival. The foraging behaviour measures of foraging distance, trip duration, path length from one parent's provisioning trip did not provided enough information to indicate the pattern of their chick's survival over the entire chick-rearing period, as expected.

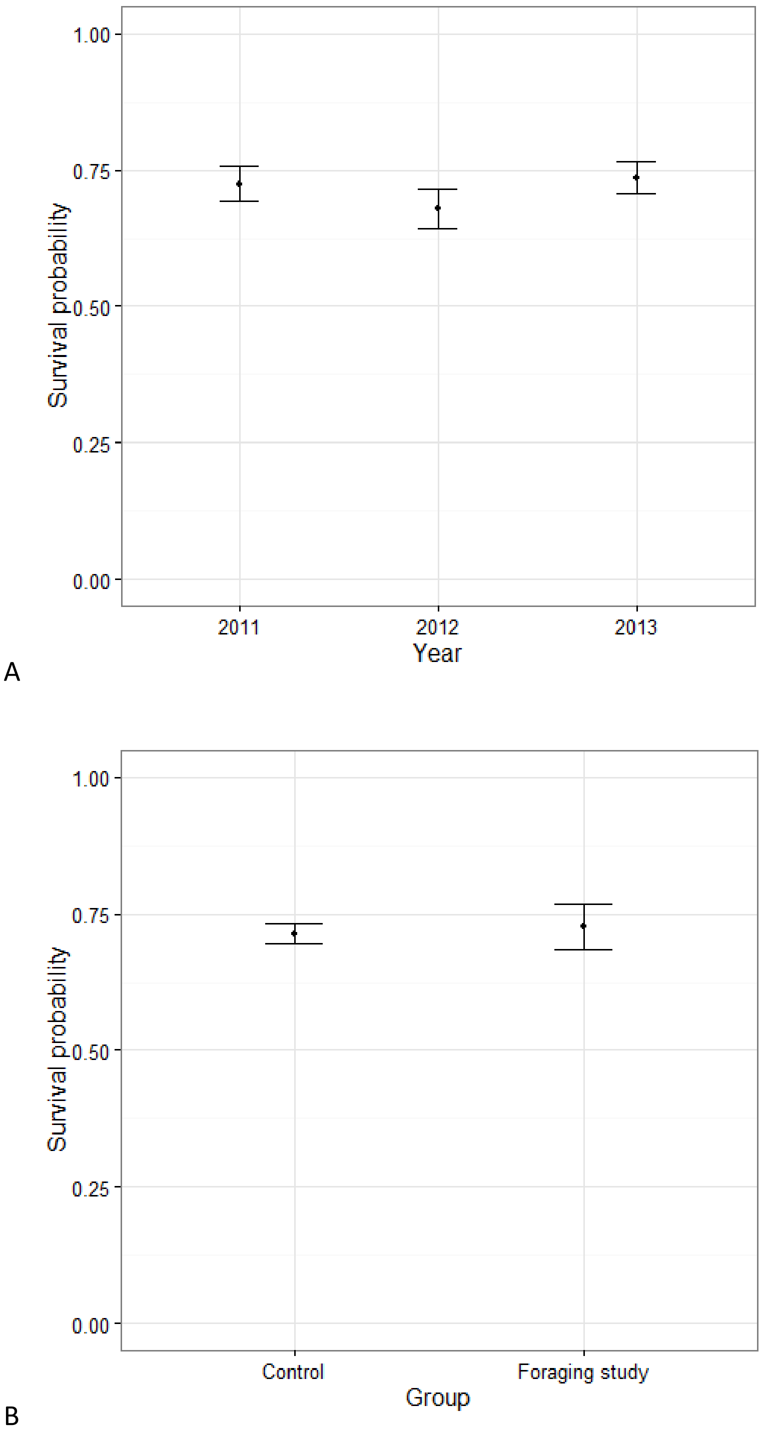

Figure 7.1. Robben Island African Penguin chick survival probabilities for the average chick rearing period of 74 days with the 95% confidence intervals for chicks in nests under vegetation for (A) the chicks in the colony which only had nest checks for breeding success monitoring in 2011 (N = 217), in 2012 (N = 203) and 2013 (N = 218), and (B) control chicks in the colony (N = 638) and the foraging study (N = 113) with all years combined.

Foraging distance and breeding attempt success results

We followed 72 breeding attempts to outcome, for which 65 had a foraging distance obtained when the chick(s) were small. The average foraging distance of the 44 successful attempts was 10.6 km while the average of the 21 unsuccessful attempts was 15.1 km. The average difference was 4.5 km (95% CI: −11.1 - 2.2 km); the Welch's *t*-test found this difference was not significant ($t_{21.8} = -4$, p = 0.18). However, the permutation test showed the difference in means was unusually large in comparison to the sorted randomized differences. Only 89 mean differences exceeded the true difference out of 10 000 permutations. Thus, the true difference falls in the top 0.9%, indicating that the means were significantly different (p = 0.009). This result was explained by a difference in distributions (Fig. 7.2). While the medians of foraging distances were both 9.5 km, the inter-quartile range of foraging distance was larger for unsuccessful birds (Fig. 7.2). The difference in the foraging distance inter-quartile ranges between penguins of successful and those that failed was 4.7 km. This difference in comparison to the sorted randomized distribution is exceptionally large, falling in the top 1.53% of the 10 000 differences; only 153 differences exceeded the true difference between the inter-quartile ranges which showed they are significantly different (p = 0.02). It indicated there was larger spread in the foraging distances of penguins that failed to raise chicks.

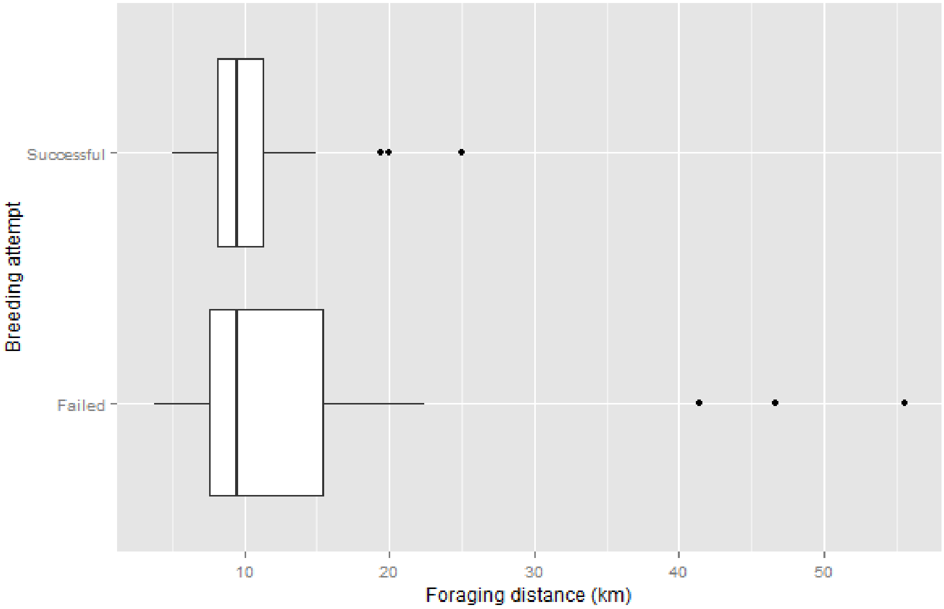

Figure 7.2. Box and whisker plots showing 65 African Penguin breeding attempt outcomes as explained by foraging distance of one of the pair's at-sea provisioning trip for small chicks. The breeding attempts resulted in 21 failures and 44 successful attempts, in which at least one chick fledged. The midline is the median, the box extends to the lower and upper quartiles and the whiskers extend to the extremes within the inter-quartile range, the circles are outliers.

Foraging behaviour and reproductive output results

There were 53 birds that had two chicks in the nest at deployment and the nests of 46 of those were followed to nest outcome. The foraging distance mean ± SD of penguins that subsequently failed to fledge any chicks was 14.2 ± 14.0 km (N = 12), one chick was 9.5 ± 2.5 km (N = 6) and two chicks was 10.2 ± 3.5 km (N = 28) (ANOVA: $F_{2,43} = 1.30$, p = 0.30) (Fig. 7.3). The permutation test with 10 000 repetitions showed foraging distance did not differ significantly between groups of birds that had different reproductive output (p = 0.26). These findings indicated that foraging distance from a foraging trip of one parent did not indicate the subsequent reproductive output.

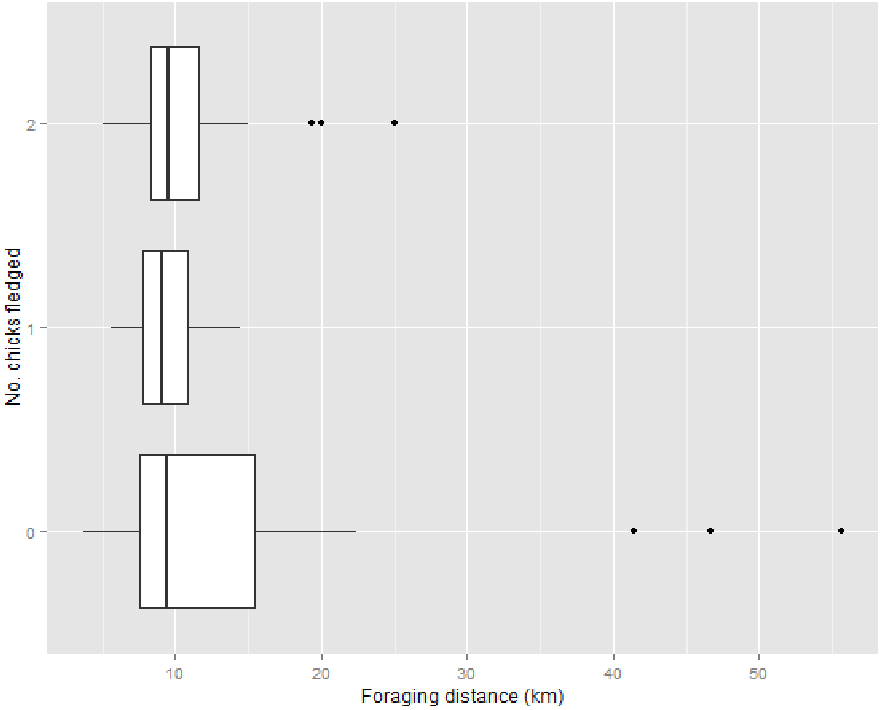

Figure 7.3. Box and whisker plots of reproductive success (the number of chicks fledged) as explained by foraging distance of 43 African Penguins that had two small chicks at the time they were equipped with a GPS-TDlog device for one foraging trip at-sea. Reproductive success outcomes were zero (N = 12), one (N = 6) and two (N = 28) chicks fledged. The midline is the median, the box extends to the lower and upper quartiles and the whiskers extend to the extremes within the inter-quartile range, the circles are outliers.

Discussion

Seabird chick growth can be highly plastic; delays in growth (Boersma 1986, Barrett and Rikardsen 1992, Chiaradia and Nisbet 2006) and development (Moe et al. 2004) are possible. In African Penguin chicks, growth rates were shown to increase and decrease with experimental changes in diet (Heath and Randall 1985) and delayed chick growth and plumage development have been observed *in situ* (van Heezik and Seddon 1992). Temporal variation in growth rates is high within African Penguin colonies (Sherley 2010). This plasticity allows seabird chicks to extend survival when feeding conditions are suboptimal and can be interpreted as an adaptation to variable prey resources.

Identifying the relationships between parental provisioning and chick survival in penguins is critical to understanding how changes in food availability impact breeding success (Rey et al. 2007). Reproductive success has been linked to food availability in the African Penguin (Crawford et al. 2006, Sherley et al. 2013). While there can be inter-annual variation in breeding success at Robben Island (Crawford et al. 2006, Sherley et al. 2013), I did not find evidence of it between the years of this study (Fig. 7.1A). Chick survival appeared comparable or higher than documented in previous years, with the exception of 2007 in Sherley et al. (2013b), indicating African Penguins were acquiring sufficient resources to raise chicks even when fish abundance varied within and between years (Chapter 4). Whether the relatively consistent high chick survival is related to the island's closure status requires further investigation. On the south coast, in Algoa Bay, a purse-seine fishery closure around the largest African Penguin colony of St. Croix initially decreased foraging effort (Pichegru et al. 2010), but no difference in chick survival was observed (Pichegru et al. 2012). Pichegru et al. (2012) proposed the lack of change to be due to the small size of the closed area and an increased fishing pressure at the borders. Yet, there is evidence that chick survival improves at Robben Island with closure status (Sherley et al. 2015).

Considerable care is needed with interpretation of studies investigating human effects to infer correct management implications (Bejder et al. 2009). While investigator disturbance can reduce penguin chick survival in Adélie Penguins (Giese 1996), other studies indicate it does not always reduce breeding success (Hull and Wilson 1996, Ballard et al. 2001, Vertigan et al. 2012). Adélie Penguins with smaller external device attachments that made up ≤ 1% of the penguin's cross-sectional area and attached for a longer period (>20 days) for multiple trips did not differ in nesting success when compared to that of control birds in the same colony (Ballard et al. 2001). Magellanic Penguin chick survival also did not differ between nest samples in tourist-visited and non-tourist visited areas at a colony with a long history of tourism, Punta Tombo, and one where eco-tourism is relatively new, San Lorenzo (Villanueva et al. 2012). In a study with Royal Penguins (*Eudyptes schlegeli*) and Southern Rockhoppers (*E. Chrysocome*), the number of active nests following monitoring from incubation to crèche did not differ between experimental nests (with nest visits and weekly chick measurements) and paired adjacent control nests which were monitored from a distance (Hull and Wilson 1996).

Human passage through an African Penguin colony can hinder reproduction by increasing the chances of adults abandoning nests with eggs and nest prospecting (Hockey and Hallinan 1981). Chicks also react to human passage through transects by flight response, standing up, and increased preening activity (Hockey and Hallinan 1981). Our finding that survival during the chick-rearing period did not differ between chicks monitored in the colony and the foraging study group which were subjected to more frequent disturbance indicated that the cost of those added disturbances did not increase mortality events prior to fledging (Fig. 7.1B). This finding is consistent with current investigations comparing chick body condition between regularly and irregularly disturbed areas of the Robben Island colony (Barham and Sherley 2013). However, there could still have been physiological costs that could impact juvenile mortality at a later life stage. In Magellanic Penguin, chick stress responses depend on their age and previous exposure to humans, yet even young chicks at hatching have a robust stress response (Walker et al. 2005). Experimental studies with captive Black-legged Kittiwake (*Rissa tridactyla*) chicks have shown that elevated levels of stress hormone, corticosterone, in seabird chicks can provide benefits for survival, such as increasing aggression and begging behaviour but it can also result in long-term developmental costs (Kitaysky et al. 2003). Investigation into the physiological stress of research activities on African Penguin chicks is warranted.

Energetic and behavioural models indicate device effects are dependent on bird body condition and food abundance (Wilson et al. 2015); it is therefore likely that impacts on chick rearing from handling and disturbance from the foraging research are not static but dependent on both extrinsic and intrinsic factors. In the Little Penguin (*Eudyptula minor*), there is some evidence that there could be a handling effect on fledging mass only in certain years (Vertigan et al. 2012). Our study did not assess fledging mass because the crèching behaviour observed in some African Penguin chicks (Barham et al. 2007) and the variability in fledging period (Sherley et al. 2013) make this parameter difficult to quantify accurately. Nevertheless, environmental conditions could impact the sensitivity of penguins to investigator disturbance.

The selective sampling that took place in the foraging research group restricts us from making a causal statement on the devices and disturbance effects. To make a causal statement one needs to have identical sampling (Authier et al. 2013). Nevertheless, the fledging success of chicks in the foraging research group did not differ from that of the chicks in the colony. Considering chick survival success was comparable, it seems likely any relationships found in the foraging study group between parental provisioning behaviour and chick survival reflected those of the rest of the colony.

The foraging behaviour of a provisioning trip of one parent when chicks were small did not explain the variation in chick survival. This is not surprising considering it is only a small sample of provisioning over the chick-rearing period and mortality from starvation is more likely to occur in chicks over 50 days old (Seddon and van Heezik 1991). African Penguin chicks reach the maximum energy requirement of 1,787 kJ/d at 53 days old (Bouwhuis et al. 2007). Considering the chicks of the equipped birds were younger than 50 days old their energy requirements would have been lower. This may also explain why sampling at this timeframe provided enough information to signal a link between foraging behaviour with breeding success but not at the level of reproductive output.

Foraging behaviour can be linked to reproductive success in provisioning penguins (Hennicke and Culik 2005, Boersma and Rebstock 2009, Boersma et al. 2015). However, studies also link reproductive success to diet in seabirds such as in Herring Gulls (*Larus argentatus*) (Pierotti and Annett 1990) and in Adélie and Chinstraps Penguins (*P. antarctica*) (Lynnes et al. 2004). Foraging behaviour and diet can vary geographically (Tremblay and Cherel 2003, Wilson et al. 2005) and there can be diet differences and shifts in response to environmental changes which can influence prey acquisition (Takahashi et al. 2003, Kowalczyk et al. 2015). Food availability plays a role in determining reproductive success (Olsson 1997, Croxall et al. 1999, Crawford et al. 2006, Sherley et al. 2013) and foraging behaviour can vary depending on the breeding stage (Charrassin et al. 1998), year and season (Charrassin et al. 1999, Clarke et al. 2002, Rey et al. 2007). A long-term consideration is that foraging ranges may shift with changes in the marine environment driven by climate change (Péron et al. 2012). Geographic environment can affect diet and foraging behaviour, which can in turn impact chick growth and reproductive success (Tremblay and Cherel 2003, Kowalczyk et al. 2015). Contrary to findings that increased foraging distance decreases reproductive success in Magellanic Penguins (Boersma and Rebstock 2009), Little Penguins at Port Phillip Bay in Australia had higher reproductive success with larger foraging ranges which can be explained by a shift in diet (Kowalczyk et al. 2015). At that site, there can be an Anchovy prey source from the Yarra River (Kowalczyk et al. 2015). To my knowledge, such freshwater food sources are not available for African Penguins so this type of anomaly is unlikely.

Foraging distance in relation to breeding success was investigated in two ways: at a per nest scale for breeding attempt and at a per chick basis of reproductive output. To address breeding attempt success, I included nests that had already lost one chick prior to deployment whereas in terms of the reproductive output, I removed those nests. In this way, sample sizes were not the same. It is possible that the penguins that had already lost a chick were less experienced breeders, or had a nest type more exposed to the elements or that their nest had already been identified by a predator. There are several reasons that breeders might vary in their capacity to rear chicks. A penguin's experience can play a role in breeding success; breeding age and pair bond duration is related to productivity (Nisbet and Dann 2009). Carry-over effects from the previous season can play a role in an individual's breeding state (Harrison et al. 2011). There may also be carry over effects in terms of adult mass from the non-breeding period, as in Little Penguins, where body mass in the season prior to breeding influenced breeding timing for both sexes and breeding success for males (Salton et al. 2015). Evidence is accumulating that African Penguin mass at the onset of breeding affects breeding success (Tol et al. 2013).

The foraging distance of one foraging trip of one of the parents is a brief snap shot of the parental care invested in chick-rearing. Despite this, there was evidence of a link between the parent's foraging distance and subsequent breeding success. Penguins that were unsuccessful in fledging a chick had greater mean and inter-quartile range in foraging distance. The signal might have been stronger if I was able to sample the behaviour of parents provisioning older chicks at peak energy demands and gather multiple trips as in Magellanic Penguin investigations using satellite transmitter tags (Boersma et al. 2015). A strong predictive link with reproductive success was found in Magellanic Penguins when chicks were older than 30 days (Boersma and Rebstock 2009). This could also explain why I found evidence of differences in foraging distance between birds that had successful and unsuccessful breeding attempts but not at the level of the number of chicks fledged. Also, automated monitoring systems of Adélie Penguins show longer foraging trip durations of females during chick-rearing are negatively correlated with breeding success (Clarke et al. 2002).

A further consideration that I could not account for is predation. Feral cats can take small chicks (Seddon and van Heezik 1991, Crawford et al. 1995, Sherley et al. 2012a, Weller et al. 2014). Predation can mask relationships between foraging distance and reproductive success (Boersma and Rebstock 2009). However, a feral cat eradication programme has been in place on Robben Island since 2006 and while their numbers have been reduced, the existence of feral cats on the island persists (de Villiers et al. 2010, pers. obs.). A feral cat was documented with a camera trap within 2.5 m of a penguin nest in April 2012.

There are other measures of parental care that influence chick growth and survival patterns such as provisioning rates (Numata et al. 2000, Takahashi et al. 2003, Chiaradia and Nisbet 2006) and nest attendance (Numata et al. 2004, Chiaradia and Nisbet 2006). Provisioning frequency can be more influential than foraging effort on offspring growth rates (Takahashi et al. 2003). Investigations into provision rate may prove preferable as they could be conducted with non-invasive methods and could capture information of multiple provisioning trips.

It would be worth examining whether the same individuals are consistently good at provisioning for their chicks or are environmental factors determining breeding success. It is likely to be a mixture of both. In Adélie Penguins inter-individual and inter-pair differences in foraging effort as time spent diving per day are consistent within a breeding season (Takahashi et al. 2003). Environmental conditions can be linked to reproductive investment (Dehnhard et al. 2015). In seabird populations, generally a portion of individuals have higher breeding success and contribute more to population growth and so identification of such individuals has conservation implications (Moreno 2003).

Caution is needed in using foraging behaviour as an indicator because it does not always predict colony growth rates (Mullers and Navarro 2010). Many factors are involved in population dynamics of African Penguin colonies (Crawford et al. 1999, Weller et al. 2014, Ludynia et al. 2014) and whether foraging distance of provisioning African Penguins could be used as an indicator of colony breeding success probability requires further investigation with more dissimilar years to identify whether foraging distance could be used as leading indicator of years of lower reproductive success.

Conclusions

Chick survival at Robben Island was comparable during the three years of the study when the island closure was in place. Survival probabilities were comparable between the chicks involved in the foraging study and control chicks that just had regular nest checks. While costs of more frequent nest checks, device deployments to a parent and handling may exist, this chapter showed they did not depress survival to fledging more than regular nest checks. The variation in chick survival was not explained by the foraging behaviour of one parent's provisioning trip when the chicks were small. Nevertheless, the foraging of penguins that had unsuccessful breeding attempts had significantly longer trip distances and inter-quartile ranges. Further investigation is needed to determine whether foraging distance can be a leading indicator of breeding success at a colony level.

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Chapter 8

Thesis Conclusions

Summary and synthesis

The purpose of this research was to examine the foraging behaviour of endangered African Penguins (*Spheniscus demersus*) rearing chicks at the Robben Island colony, identify which factors influence their foraging behaviour and explore links between foraging behaviour and breeding success. The thesis is composed of six data chapters; the first two present morphological indicators and the subsequent four all address factors relevant to adult provisioning behaviour. The study was conducted by equipping adults provisioning small chicks with GPS temperature depth logger devices for one foraging trip. Where possible, deployments were timed to track penguins at the same time as fine-scale hydro-acoustic surveys. Chick body condition and breeding success monitoring took place in the colony during the study as well as diet sampling of breeding adults.

The African Penguin diving behaviour and movement trajectories are described and the variability of foraging behaviour and foraging areas explored in Chapter 4. Annual differences were found in dive behaviour and foraging effort. The new morphological tools developed in Chapter 2 and Chapter 3 allowed for a comparison of intrinsic factors of adult penguins and foraging behaviour. Intrinsic factors were not as influential on foraging behaviour measures as extrinsic factors such as chick brood mass at deployment and local pelagic fish abundance (Chapter 4 and Chapter 5). Prey availability provided an explanation for the annual differences observed in foraging behaviour (Chapter 4). The local prey abundance explained more than half of the time penguins spent diving and some of the variation in foraging distance from the island (Fig. 5.7). Penguins spent more time diving when local prey abundance was low (Fig. 5.7). Foraging distance from the island was more variable at times of low prey abundance (Fig. 5.7).

Over the three years of the study, 100% of the core foraging area and 96% of the foraging home range of breeding African Penguins were within the closure zone which extended 20 km out around Robben Island, indicating African Penguins raising chicks make consistent use of that area (Fig. 8.1). Even though foraging areas always included areas within 20 km of the island, when pelagic fish abundance was lower penguins also foraged at distances further away from the island (Table 4.4, Fig. 4.13, Fig. 5.4).

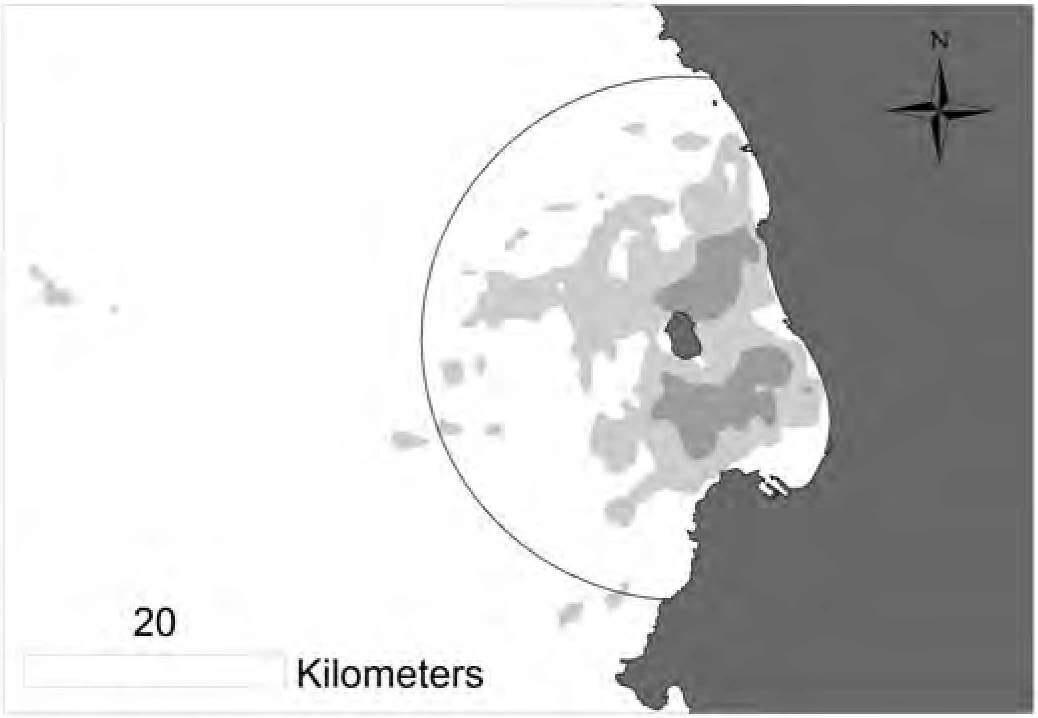

Figure 8.1. African Penguin core foraging area in medium grey and foraging range area in light grey in from the foraging dives collected in 2011, 2012 and 2013 from breeding adults provisioning small chicks. Land is in dark grey. During those years a purse-seine fisheries closure zone extended around the island out to 20 km radius from the marked black point on the Robben Island. The foraging home range area outside of the 20 km zone was 13.5 km^2 while the total was 347.5 km^2.

This thesis has several other important findings:

- Foraging effort was higher in 2011 when there was a lower availability of preferred prey around the island (Chapter 5).
- Mean wave height and direction had weak negative correlations to foraging behaviours (Fig. 4.21), while local pelagic fish abundance had strong negative correlations to foraging behaviours (Fig. 5.6) (Chapter 4 and Chapter 5).
- At Robben Island the foraging areas and behaviour of the sexes are similar (Chapter 4).

- Chick body condition was positively related to local pelagic fish abundance (Fig. 6.7) and the percentage of Anchovy (*Engraulis encrasicolus*) in the diet (Fig. 6.9) (Chapter 6).
- Penguins with unsuccessful breeding attempts had higher mean foraging distance and larger inter-quartile ranges of foraging distance (Chapter 7).
- Survival probabilities were comparable between chicks in the foraging study and control chicks (Fig. 7.1).
- Chick survival at Robben Island did not differ between years despite the variability in prey availability around the colony identified by the hydro-acoustic surveys and penguin diet sampling (Fig. 5.4 and Fig. 7.1).
- The foraging behaviour measures of one parent on a single foraging trip did not provide enough information to indicate chick survival; however, there was evidence that foraging distance could indicate breeding success but not reproductive output (Chapter 7).

The two new and useful morphologically based tools presented were used to determine the sex and body condition of adult penguins. The Farah discriminant function – presented in Chapter 2 – provides a simple method that can be used to sex African Penguins throughout their South African range using established bill length and depth measurements. It was used to sex African Penguins in this foraging study. In Chapter 3, I showed how quantile regression techniques can be used to allow for a minimum number of measurements to be compared to a large data set of morphometrics. This approach was used to develop an adult African Penguin body condition index and its advantages were explained. This index was used in Chapter 4 to compare adult body condition to foraging behaviour and was able to demonstrate these were not related over the range of body condition values considered there (Chapter 4).

Applications

The morphological tools presented to investigate African Penguin foraging behaviour also have further applications. Identification of sex and body condition of penguins in the field can improve behavioural studies and improve capacity towards integrated population modelling. The comparison of bill morphology at different South African colonies confirmed that the Farah discriminant function for sexing birds from bill measurements with the established depth measurement (Table 2.3) and the existing discriminant function (Pichegru et al. 2013) can be applied throughout the South African range of the species. Their accuracy is similar provided the appropriate bill depth measurements are used.

With a random sampling protocol and consistent depth measurement, a discriminant function could be used to estimate sex ratios in the field (Chapter 2).

The adult body condition index using culmen length, mass and quantile regression techniques (eqns. 3.1-3.5) could be used to improve the release criterion of rehabilitated African Penguins and to compare the body condition of adults measured in the field spatially or temporally. The timing of breeding bird foraging trips indicates the best times for adult body measurements is in the morning to avoid biases from prey loads (Chapter 3). Adult body condition monitoring could be initiated to compare penguins breeding at different colonies.

The chick body condition index was extended to small-sized chicks using a non-linear quantile regression (Chapter 6), following Braby (2011). It allowed for more data to be used in investigations of chick body condition in relation to diet composition and local prey abundance. It could be used in this way to investigate chick condition at other colonies. The calculation details are provided in the Supplementary Materials S2. The approach could also be applied to other species.

The quantile approach of the body condition index has the advantage of being easy to interpret biologically and it can be applied even if there is heteroscedasticity in the relationship between mass and a size variable. The body condition index could be applied to other species with empirical validation. Many body condition indicators are in use (Labocha and Hayes 2012); the body condition index could be compared to other body condition indicators in use in more detail.

This thesis has ramifications for African Penguin monitoring. There is considerable intra-annual variation in African Penguin foraging behaviour as well as local pelagic fish abundance throughout the breeding season. This must be taken into consideration when sampling protocols are developed and data are analysed for estimates to be considered representative of a breeding season. Nest checks following deployments can provide further information for understanding the links between behaviour and population dynamics (Chapter 7). Diet monitoring can contribute to our understanding of chick body condition (Chapter 6). This study's findings show efforts for simultaneous sampling have merit and should be increased. Collaborations between government departments and researchers for the synchronisation of data collection are beneficial to investigations seeking to address predator-prey relations in dynamic marine ecosystems (Chapter 5 and Chapter 6).

The findings also have conservation applications. The foraging data was used to provide comments to the South African Government in respect to the Robben Island Marine Protected Area (MPA) (Government Gazette of South Africa 2016). The restricted and controlled zones together enclose an area in which 8,853 African Penguin foraging dives were observed, 50% of the total dives (Fig. 8.2). The Robben Island MPA encloses 50% of the penguin core foraging area and 52% of the foraging home range observed (Fig. 8.3). This indicates that the Robben Island MPA could provide protection to approximately half of the marine areas used consistently by endangered African Penguins breeding at Robben Island. Reinstating the closure area should be considered. Adding the closure zone to the Robben Island MPA would increase coverage to the entire core foraging area of the African Penguins provisioning chicks at Robben Island.

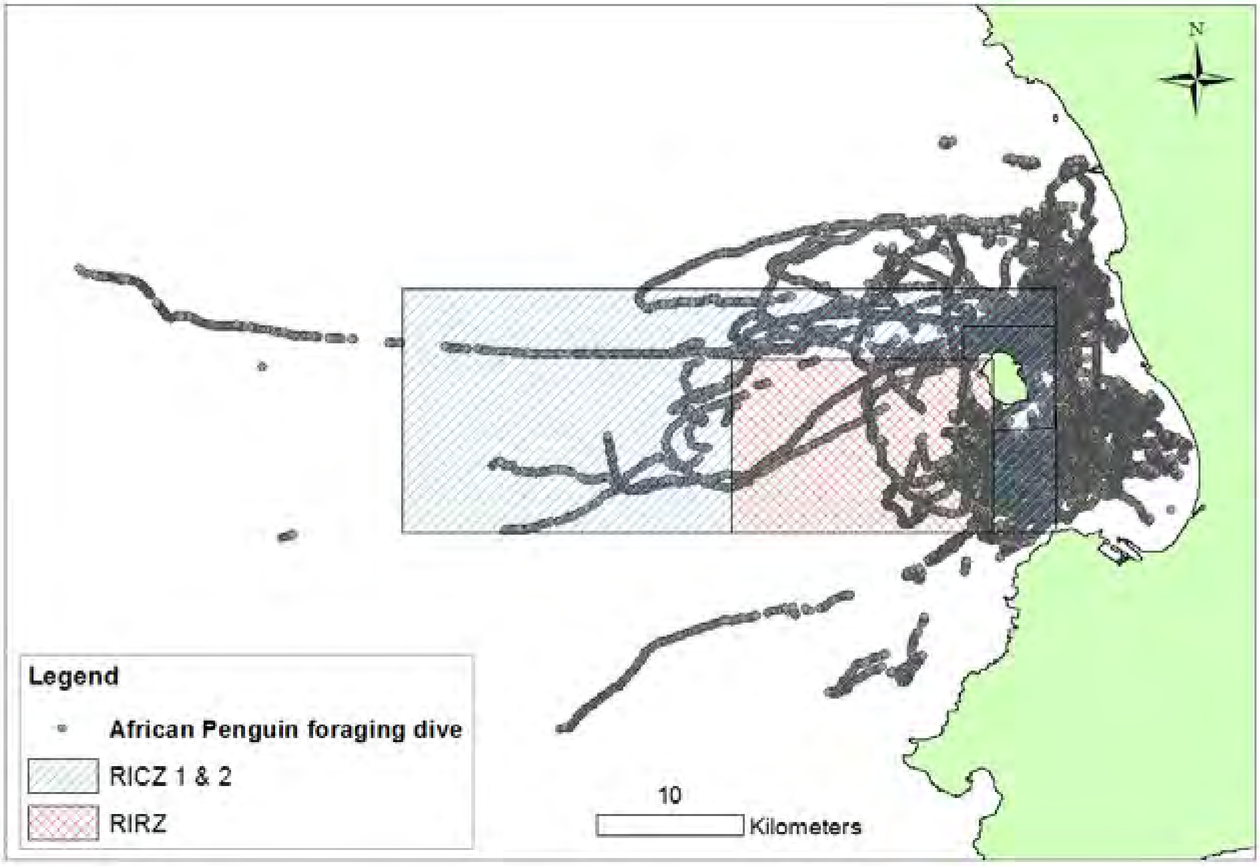

Figure 8.2. Robben Island Marine Protected Area with the Robben Island Controlled Zones (RICZ) in blue stripes and the Robben Island Restricted Zone in red hash marks over the 17,618 African Penguin foraging dives from 75 individuals provisioning for chicks. The Robben Island MPA was gazetted in 2016 while the penguin dives were collected in the breeding seasons of 2011 to 2013 when a 20 km closure to purse-seine fishing was in place around the island.

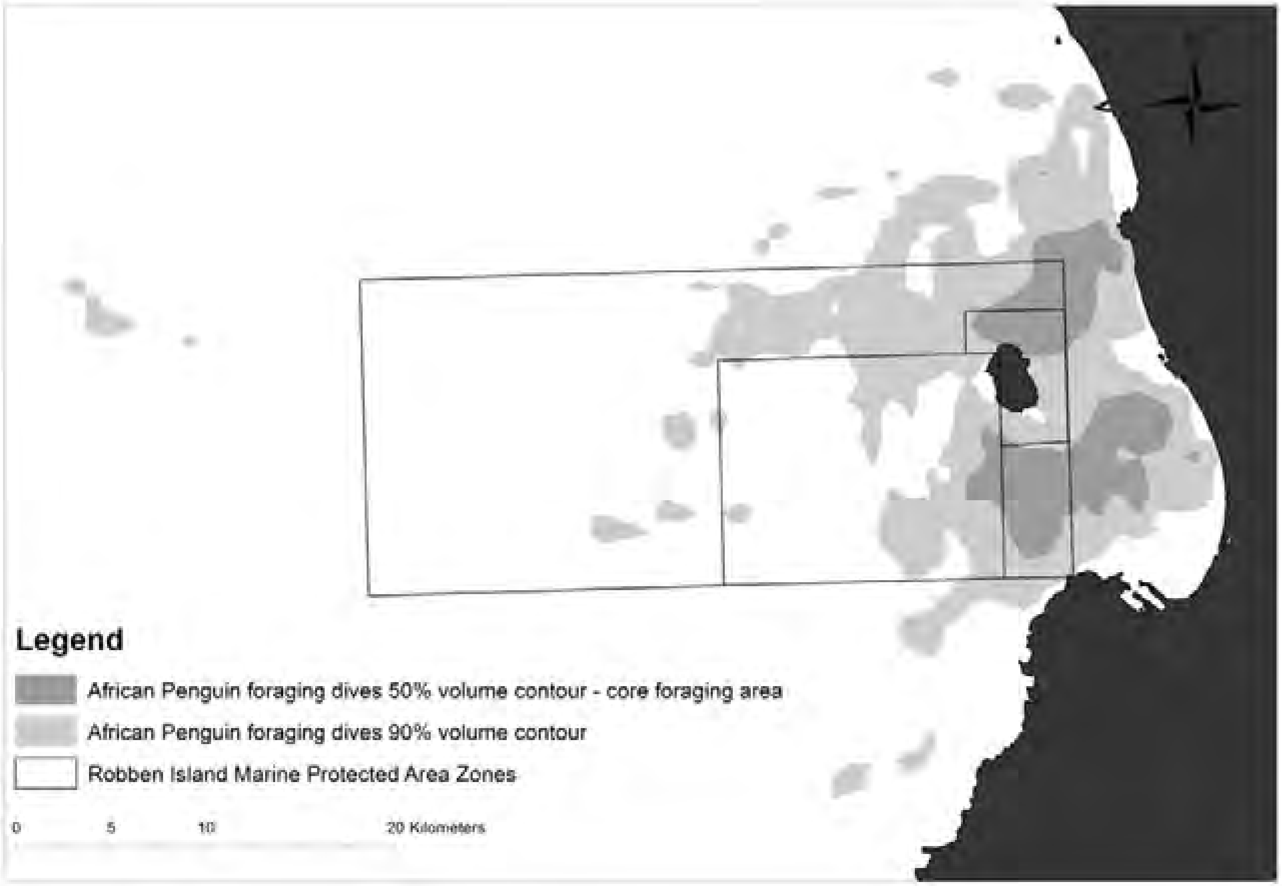

Figure 8.3. The core foraging area and foraging home range of 75 African Penguins provisioning chicks when a fisheries closure zone out 20 km around the island was in place from 2011 to 2013. Robben Island Marine Protected Area (MPA) as gazetted in 2016 is overlaid and encloses 39 km^2 of the core foraging area which is 78.3 km^2. It also encloses 180 km^2 of the foraging home range which is 347.5 km^2.

Conservation efforts need to be multi-fold and address a variety of threats to halt the declines seen in the African Penguin at this colony (Weller et al. 2014) and as a species (Government Gazette of South Africa 2013). The foraging areas around the island identified are used during chick provisioning and are important for this colony. Marine protected areas provide one avenue of protection. Considering local prey abundance and the percentage of Anchovy in the diet are related to chick body condition (Chapter 4), spatial fisheries management is also needed because of the fluid and connected nature of the ocean environment. Monitoring of chick body condition is also necessary for the chick bolstering efforts (Sherley et al. 2014) and needs to be continued in conjunction with other monitoring programs and conservation initiatives.

Future research directions

Additional tracking, in combination with fine-scale pelagic fish surveys, would provide further insight into prey density and abundance thresholds at which penguins change their foraging behaviour while provisioning chicks. Comparisons using a greater number of fine-scale surveys, or more accurate estimates of local biomass, are required to identify functional relationships. A longer time series than three years, or years with more variation in breeding success, are needed to ascertain whether foraging behaviour can act as a leading indicator of the population dynamics of the colony.

The fine-scale surveys show pelagic fish abundances around the island are highly variable even within years (Chapter 5); yet, chick survival was comparable during the years of this study (Chapter 7). There is evidence that relatively high chick survival during these years can be explained by the closure out to 20 km (Sherley et al. 2015). Whether a difference in foraging behaviour during closure can also be detected is under investigation. Finding links with foraging behaviour is complicated by the small numbers of birds that can be tracked for one trip, the short-term nature of foraging behaviour and that it is influenced by highly variable local prey availability (Chapter 5).

Questions remain about how African Penguins locate their prey. Dimethyl sulfide (DMS) has been suggested as a chemical cue for African Penguin (Cunningham et al. 2008, Wright et al. 2011) and other seabirds (Nevitt and Bonadonna 2005). The technology exists for trace analysis of DMS and dimethylsulfoniopropionate (DMSP) in natural waters (Nagahata et al. 2013). Whether the distribution of DMS matches that of prey could be tested with methods described in Nagahata et al. (2013) during fine-scale pelagic-fish surveys. This could provide confirmation for the potential of DMS as a sensory landscape that indicates prey locations to upper-trophic level marine predators like penguins.

The foraging areas and behaviour of the sexes were comparable at Robben Island (Chapter 4); this is contrary to findings at Eastern Cape colonies (Pichegru et al. 2013). It would be worthwhile to re-examine the sex-specific spatial differences found at Eastern Cape colonies with an individual minimum convex polygon approach. I recommend using this technique at other colonies as well. If the sex-specific differences are confirmed at Eastern Cape colonies but not at Western Cape ones it would be interesting to investigate the possible drivers suggested in Chapter 4 for those behavioural differences. It could be possible that other factors which have not been addressed such as immunocompetence, age or breeding experience could be relevant to foraging behaviour.

In terms of researcher impacts, chick survival was similar between chicks monitored in the colony and the chicks in the foraging study, which were handled and had been subjected to more frequent nest checks (Chapter 7). Even though a difference in survival was not detected, it is possible there could be physiological differences between the chicks. Investigations into baseline levels of, and variability in, stress hormones are warranted for this species. Increased stress hormones in seabird chicks can have different effects at different life-history stages (Kitaysky et al. 2003). Also, investigations into stress response with the same African Penguin adults could be conducted to confirm whether the species habituates to human approach as suspected, following approaches used with endangered Yellow-eyed Penguins (*Megadyptes antipodes*) (Ellenberg et al. 2009).

Further investigation into feed frequencies, time away from the nest and time guarding chicks could provide additional information on parental care and chick provisioning behaviour. Such information could be looked at independently or in combination with tracking device deployment. Camera trap nest monitoring could be used to investigate this in a non-invasive way; a few camera trap trials were made during the foraging research and were able to capture the return time to a nest of an equipped bird (Fig. 8.4).

Figure 8.4. Camera trap photo of an equipped African Penguin which identified the return time of the penguin to its nest from the date and time stamps (bottom right of image). It agrees with the GPS data which indicated the penguin returned to within 5 m of the nest at 17:35. This indicates camera traps have potential for monitoring foraging trip durations.

In this way, African Penguin provisioning research could move towards non-invasive monitoring techniques, as with efforts to move towards non-invasive and fully-automated demographic monitoring (Sherley et al. 2010).

This thesis identified several relationships that will be useful for ecosystem modelling and moving towards the capacity for integrated population modelling of the species. In particular, the positive relationships between chick body condition with local prey abundance and percent mass of Anchovy in the diet. Investigations are needed on how fluctuations in local prey abundance influence population dynamics. Studies have incorporated pelagic fish abundance from large scale hydro-acoustic surveys into demographic modelling (e.g., Sherley et al. 2013b, Weller et al. 2014, Ludynia et al. 2014), yet the local pelagic fish abundance might be more influential on reproduction and survival. A relationship was not found between adult body condition and chick body condition, possibly because there was not enough variance in the adult condition to identify one. This could be examined by sampling more breeding individuals and their chicks in the colony.

Further investigation is needed to identify how foraging behaviour relates to adult survival and maintenance but our knowledge of foraging behaviour outside of the breeding season remains limited. Penguin tracking has been conducted of juveniles post-fledging (Sherley et al. 2013a) and adults pre-moult (Harding 2013) but not post-moult to identify where penguins forage to replenish their body reserves. These foraging areas are likely to be critically important for penguins in respect to survival. Harding (2013) conducted a trail deployment of a PTT on a penguin post-moult in captivity indicating it might be a feasible method. However, there are serious ethical considerations that such deployments might put individual survival at risk in the wild. Further trials with captive birds are warranted. Whether studies could be conducted to identify post-moult foraging areas without putting study individuals' survival at risk has yet to be determined. Alternative ways of identifying foraging areas outside of the breeding season require consideration.

Fine-scale investigations of pelagic fish around penguin colonies with hydro-acoustic surveys and concurrent tracking of penguin, diet sampling, chick body condition and breeding success can provide valuable insight into predator-prey dynamics. Further work remains to be conducted on pelagic fish movements, the spatial dynamics of pelagic fish and penguins and their distributions at different scales. The information is needed for integrated population dynamics modelling and for indentifying penguin-fisheries interactions. Identifying prey requirements and foraging areas can inform conservation.

Concluding remarks

African Penguin foraging behaviour when provisioning chicks and chick body condition were found to be related to the local prey abundance around the Robben Island colony. Prey availability for endangered penguins needs to be taken into consideration for effective ecosystem management. The foraging areas identified showed consistent use of the closure area. It also showed they forage within areas of the Robben Island MPA. Considering the variability of pelagic fish abundance in the system, closure areas around colonies in combination with spatial management of pelagic fish stocks and multiple conservation approaches will be needed to halt the declines of African Penguins. The importance of local prey availability and the location of foraging areas can inform stakeholders and help to identify effective conservation efforts for cohesive actions.

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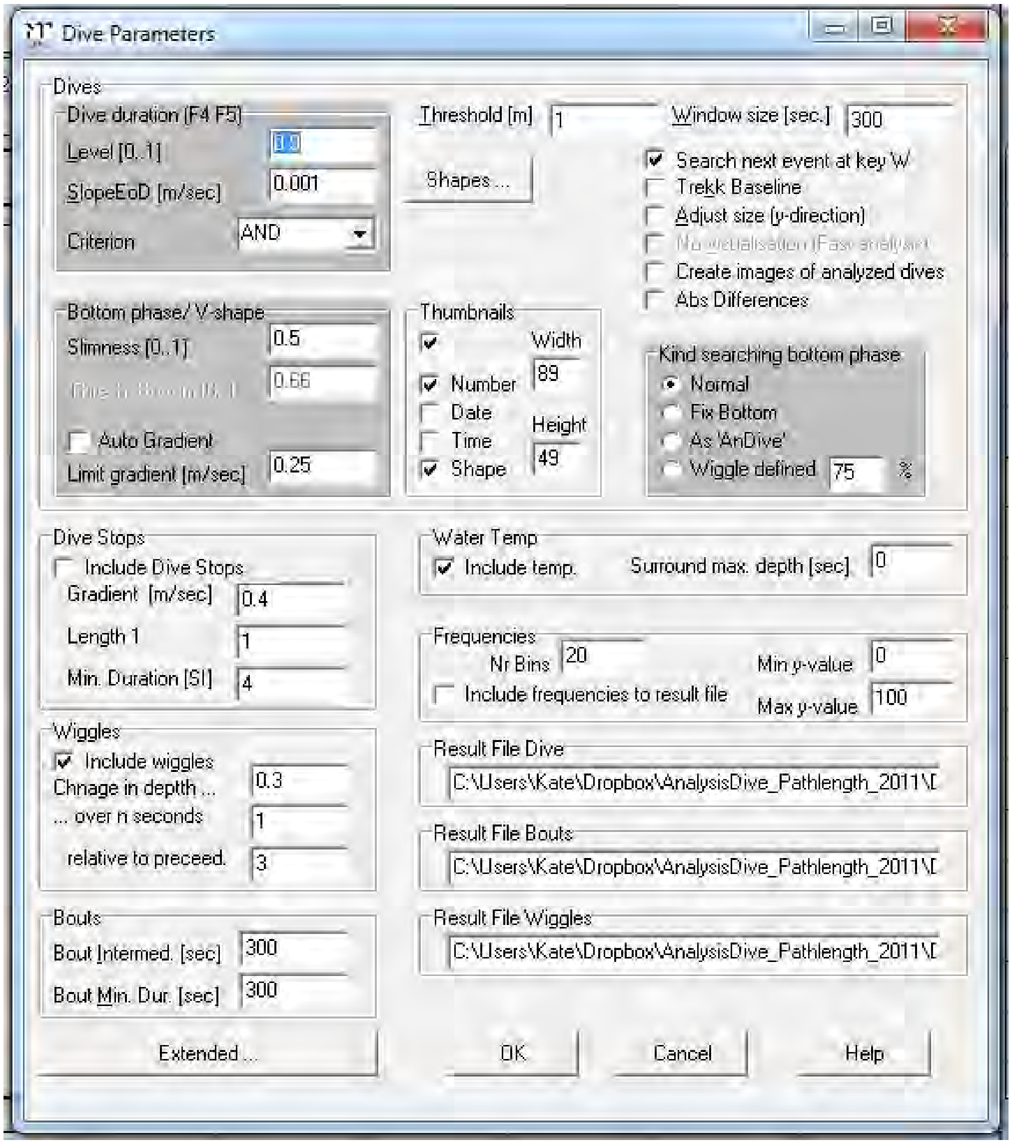
Supplementary materials

Supplement S1

Dive analysis parameters

The MTDive settings used for the African Penguin dive analysis are provided in Figures S1.1 to S1.3 should anyone wish to replicate the analysis or use the same settings.



Dive Parameters

Dives

Dive duration (F4 F5)
Level [0..1] 0.8
SlopeEoD [m/sec] 0.001
Criterion AND

Bottom phase/ V-shape
Slimness [0..1] 0.5
[illegible] 0.66
☐ Auto Gradient
Limit gradient [m/sec] 0.25

Threshold [m] 1
Window size [sec.] 300
☑ Search next event at key W
☐ Trekk Baseline
☐ Adjust size (y-direction)
☐ No visualisation (Fast analysis)
☐ Create images of analyzed dives
☐ Abs Differences

Thumbnails
☑
☑ Number
☐ Date
☐ Time
☑ Shape
Width 89
Height 49

Kind searching bottom phase
● Normal
○ Fix Bottom
○ As 'AnDive'
○ Wiggle defined 75 %

Dive Stops
☐ Include Dive Stops
Gradient [m/sec] 0.4
Length 1 1
Min. Duration [Sl] 4

Water Temp
☑ Include temp.
Surround max. depth [sec] 0

Frequencies
Nr Bins 20
☐ Include frequencies to result file
Min y-value 0
Max y-value 100

Wiggles
☑ Include wiggles
Chnage in deptth ... 0.3
... over n seconds 1
relative to preceed. 3

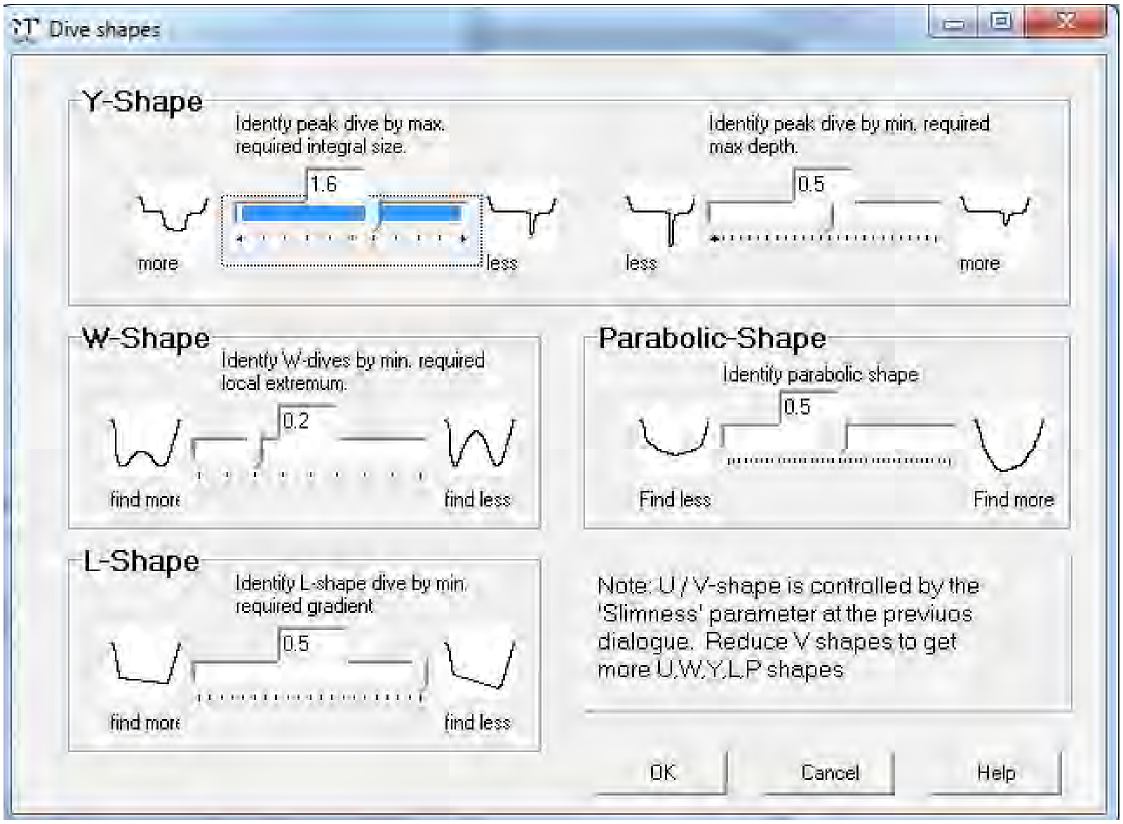
Result File Dive
C:\Users\Kate\Dropbox\AnalysisDive_Pathlength_2011\D

Result File Bouts
C:\Users\Kate\Dropbox\AnalysisDive_Pathlength_2011\D

Result File Wiggles
C:\Users\Kate\Dropbox\AnalysisDive_Pathlength_2011\D

Bouts
Bout Intermed. [sec] 300
Bout Min. Dur. [sec] 300

Figure S1.1. Parameters selected for African Penguin dive analysis in MTDive.



Identify peak dive by max. required integral size. 1.6

Identify peak dive by min. required max depth. 0.5

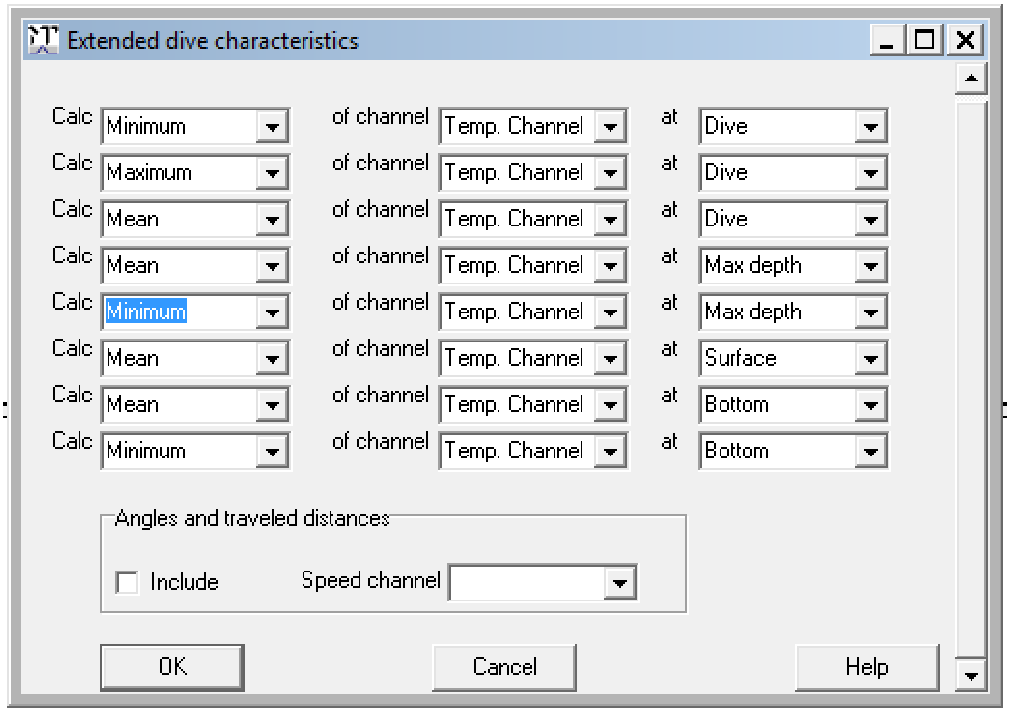
Identify W-dives by min. required local extremum. 0.2

Identify parabolic shape 0.5

Identify L-shape dive by min. required gradient 0.5

Note: U / V-shape is controlled by the 'Slimness' parameter at the previuos dialogue. Reduce V shapes to get more U,W,Y,L,P shapes

Figure S1.2. MTDive dive shape parameter default settings used for dive analysis.



Calc	Minimum	of channel	Temp. Channel	at	Dive
Calc	Maximum	of channel	Temp. Channel	at	Dive
Calc	Mean	of channel	Temp. Channel	at	Dive
Calc	Mean	of channel	Temp. Channel	at	Max depth
Calc	Minimum	of channel	Temp. Channel	at	Max depth
Calc	Mean	of channel	Temp. Channel	at	Surface
Calc	Mean	of channel	Temp. Channel	at	Bottom
Calc	Minimum	of channel	Temp. Channel	at	Bottom

Angles and traveled distances

☐ Include   Speed channel

Figure S1.3. Dive analysis parameters of the extended dive characteristics of the temperature channel.

Supplement S2

Chick body condition index extended with non-linear quantiles

A sample of 125 chicks which fledged in 2004 were measured repeatedly while they were in the nest as part of an energetics study (Bouwhuis et al. 2007). Those measurements were used to create a chick body condition index for chicks with head lengths > 75 mm (Lubbe et al. 2014). The same measurements were used to generate non-linear quantiles in GenStat (VSN International 2011) to extend the body condition index to small-sized chicks with head lengths ≤ 75 mm. Table S2.1 provides the predicted body mass at the 5% and 95% quantiles for chicks with head lengths of 38 to 122 mm for each 0.1 mm. These values were used to calculate African Penguin chick Body Condition Index (BCI) in Chapter 6. To calculate the BCI of a chick of a particular head length (mm)size one needs chick's body mass (kg) and then the predicted body mass at the 5% and 95% quantiles at that head length size. Then chick body BCI is calculated as follows,

$$\mathrm{BCI} = \frac{(\mathrm{M_i} - \mathrm{M_{5\%}})}{(\mathrm{M_{95\%}} - \mathrm{M_{5\%}})}$$

where M_i is the observed body mass of a chick i of head length x and $M_{5\%}$ and $M_{95\%}$ are the predicted body mass at the 5% and 95% quantiles, respectively, at head length x.

If the BCI value is > 1 the chick is in better body condition than the 95% quantile of those 2004 chicks while a negative BCI indicates the a chick in body condition was worse than the 5% quantile of the chicks that fledged successfully in 2004 (Lubbe et al. 2014). It provides a comparative measure with which to evaluate chick body condition.

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Table S2.1. The body mass predicted at the 5% and 95% quantiles for chicks of head length values from 38 to 122 mm by 0.1 mm from the nonlinear quantile regressions on the multiple measurements of 125 chicks at Robben Island which fledged in 2004.

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
38.0	0.044	0.063
38.1	0.044	0.063
38.2	0.045	0.064
38.3	0.045	0.065
38.4	0.045	0.066
38.5	0.046	0.067
38.6	0.046	0.068
38.7	0.046	0.069
38.8	0.047	0.070
38.9	0.047	0.071
39.0	0.047	0.072
39.1	0.048	0.073
39.2	0.048	0.073
39.3	0.048	0.072
39.4	0.049	0.073
39.5	0.049	0.073
39.6	0.049	0.074
39.7	0.050	0.075
39.8	0.050	0.075
39.9	0.050	0.077
40.0	0.051	0.078
40.1	0.051	0.079
40.2	0.051	0.080
40.3	0.052	0.080
40.4	0.052	0.081
40.5	0.052	0.082
40.6	0.053	0.083
40.7	0.053	0.084
40.8	0.053	0.085
40.9	0.054	0.086
41.0	0.054	0.088
41.1	0.054	0.089
41.2	0.054	0.090
41.3	0.055	0.091
41.4	0.055	0.092
41.5	0.055	0.093
41.6	0.054	0.095
41.7	0.055	0.096
41.8	0.055	0.095

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
41.9	0.056	0.097
42.0	0.056	0.099
42.1	0.057	0.100
42.2	0.057	0.102
42.3	0.058	0.103
42.4	0.058	0.105
42.5	0.059	0.105
42.6	0.059	0.106
42.7	0.060	0.108
42.8	0.060	0.109
42.9	0.061	0.111
43.0	0.061	0.112
43.1	0.062	0.114
43.2	0.061	0.115
43.3	0.062	0.117
43.4	0.063	0.119
43.5	0.063	0.120
43.6	0.064	0.122
43.7	0.064	0.123
43.8	0.066	0.125
43.9	0.066	0.126
44.0	0.067	0.128
44.1	0.068	0.129
44.2	0.069	0.131
44.3	0.070	0.132
44.4	0.071	0.134
44.5	0.073	0.136
44.6	0.074	0.137
44.7	0.075	0.139
44.8	0.076	0.140
44.9	0.078	0.142
45.0	0.079	0.144
45.1	0.080	0.146
45.2	0.081	0.147
45.3	0.082	0.149
45.4	0.084	0.151
45.5	0.085	0.152
45.6	0.087	0.154
45.7	0.088	0.155
45.8	0.089	0.157
45.9	0.092	0.159
46.0	0.093	0.160

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
46.1	0.093	0.162
46.2	0.095	0.164
46.3	0.096	0.166
46.4	0.097	0.168
46.5	0.099	0.170
46.6	0.100	0.172
46.7	0.101	0.174
46.8	0.103	0.175
46.9	0.105	0.177
47.0	0.107	0.179
47.1	0.108	0.181
47.2	0.110	0.183
47.3	0.111	0.185
47.4	0.112	0.187
47.5	0.114	0.188
47.6	0.115	0.190
47.7	0.116	0.192
47.8	0.118	0.194
47.9	0.119	0.195
48.0	0.121	0.197
48.1	0.122	0.199
48.2	0.123	0.201
48.3	0.125	0.203
48.4	0.126	0.206
48.5	0.128	0.209
48.6	0.129	0.211
48.7	0.130	0.213
48.8	0.132	0.215
48.9	0.133	0.217
49.0	0.134	0.219
49.1	0.136	0.221
49.2	0.137	0.223
49.3	0.138	0.225
49.4	0.140	0.226
49.5	0.141	0.228
49.6	0.142	0.231
49.7	0.144	0.233
49.8	0.145	0.235
49.9	0.147	0.236
50.0	0.148	0.239
50.1	0.149	0.241
50.2	0.151	0.243

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
50.3	0.152	0.245
50.4	0.154	0.248
50.5	0.155	0.250
50.6	0.156	0.252
50.7	0.158	0.254
50.8	0.159	0.256
50.9	0.161	0.258
51.0	0.162	0.261
51.1	0.164	0.263
51.2	0.165	0.266
51.3	0.167	0.268
51.4	0.168	0.271
51.5	0.170	0.274
51.6	0.171	0.277
51.7	0.172	0.279
51.8	0.179	0.281
51.9	0.180	0.283
52.0	0.181	0.284
52.1	0.183	0.287
52.2	0.184	0.288
52.3	0.186	0.291
52.4	0.188	0.293
52.5	0.189	0.296
52.6	0.191	0.298
52.7	0.192	0.300
52.8	0.193	0.303
52.9	0.195	0.304
53.0	0.197	0.307
53.1	0.198	0.311
53.2	0.200	0.313
53.3	0.201	0.317
53.4	0.202	0.320
53.5	0.205	0.323
53.6	0.207	0.325
53.7	0.209	0.328
53.8	0.211	0.330
53.9	0.213	0.332
54.0	0.214	0.335
54.1	0.216	0.337
54.2	0.218	0.340
54.3	0.220	0.342
54.4	0.222	0.345

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
54.5	0.223	0.347
54.6	0.225	0.350
54.7	0.227	0.352
54.8	0.229	0.354
54.9	0.230	0.357
55.0	0.232	0.359
55.1	0.234	0.362
55.2	0.236	0.364
55.3	0.238	0.367
55.4	0.240	0.369
55.5	0.242	0.372
55.6	0.244	0.375
55.7	0.245	0.377
55.8	0.247	0.380
55.9	0.249	0.383
56.0	0.251	0.386
56.1	0.253	0.389
56.2	0.254	0.392
56.3	0.256	0.394
56.4	0.258	0.397
56.5	0.260	0.399
56.6	0.261	0.403
56.7	0.263	0.406
56.8	0.265	0.409
56.9	0.267	0.412
57.0	0.269	0.415
57.1	0.271	0.417
57.2	0.272	0.420
57.3	0.274	0.423
57.4	0.276	0.425
57.5	0.278	0.428
57.6	0.280	0.430
57.7	0.282	0.433
57.8	0.284	0.435
57.9	0.286	0.440
58.0	0.287	0.442
58.1	0.289	0.445
58.2	0.291	0.448
58.3	0.293	0.451
58.4	0.295	0.455
58.5	0.297	0.458
58.6	0.299	0.461

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
58.7	0.301	0.464
58.8	0.302	0.469
58.9	0.304	0.472
59.0	0.306	0.475
59.1	0.308	0.478
59.2	0.310	0.481
59.3	0.312	0.484
59.4	0.314	0.487
59.5	0.316	0.491
59.6	0.318	0.494
59.7	0.320	0.497
59.8	0.322	0.500
59.9	0.324	0.503
60.0	0.326	0.506
60.1	0.328	0.510
60.2	0.332	0.512
60.3	0.334	0.515
60.4	0.336	0.518
60.5	0.338	0.521
60.6	0.341	0.524
60.7	0.343	0.527
60.8	0.345	0.530
60.9	0.347	0.533
61.0	0.349	0.536
61.1	0.352	0.540
61.2	0.354	0.543
61.3	0.356	0.547
61.4	0.360	0.550
61.5	0.362	0.553
61.6	0.366	0.556
61.7	0.369	0.559
61.8	0.371	0.562
61.9	0.373	0.568
62.0	0.376	0.571
62.1	0.378	0.576
62.2	0.379	0.580
62.3	0.382	0.583
62.4	0.386	0.587
62.5	0.388	0.590
62.6	0.390	0.593
62.7	0.393	0.597
62.8	0.395	0.600

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
62.9	0.398	0.604
63.0	0.400	0.607
63.1	0.403	0.610
63.2	0.404	0.614
63.3	0.412	0.617
63.4	0.414	0.620
63.5	0.421	0.624
63.6	0.425	0.626
63.7	0.428	0.629
63.8	0.431	0.632
63.9	0.434	0.635
64.0	0.436	0.638
64.1	0.439	0.642
64.2	0.442	0.645
64.3	0.445	0.649
64.4	0.448	0.652
64.5	0.451	0.655
64.6	0.453	0.659
64.7	0.456	0.662
64.8	0.459	0.666
64.9	0.462	0.669
65.0	0.468	0.673
65.1	0.471	0.676
65.2	0.474	0.679
65.3	0.477	0.683
65.4	0.480	0.686
65.5	0.483	0.689
65.6	0.486	0.693
65.7	0.489	0.697
65.8	0.492	0.703
65.9	0.495	0.706
66.0	0.498	0.710
66.1	0.500	0.713
66.2	0.502	0.717
66.3	0.505	0.721
66.4	0.508	0.725
66.5	0.511	0.728
66.6	0.515	0.732
66.7	0.518	0.736
66.8	0.521	0.739
66.9	0.525	0.743
67	0.528	0.747

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
67.1	0.531	0.750
67.2	0.534	0.754
67.3	0.537	0.757
67.4	0.540	0.761
67.5	0.541	0.765
67.6	0.544	0.768
67.7	0.547	0.772
67.8	0.550	0.776
67.9	0.553	0.780
68.0	0.556	0.784
68.1	0.559	0.788
68.2	0.562	0.793
68.3	0.566	0.797
68.4	0.569	0.801
68.5	0.572	0.805
68.6	0.575	0.808
68.7	0.578	0.812
68.8	0.581	0.816
68.9	0.584	0.820
69.0	0.587	0.824
69.1	0.590	0.828
69.2	0.593	0.832
69.3	0.596	0.836
69.4	0.600	0.840
69.5	0.603	0.844
69.6	0.608	0.848
69.7	0.610	0.854
69.8	0.613	0.857
69.9	0.616	0.860
70.0	0.619	0.864
70.1	0.622	0.868
70.2	0.625	0.872
70.3	0.628	0.877
70.4	0.631	0.881
70.5	0.635	0.885
70.6	0.638	0.890
70.7	0.641	0.895
70.8	0.644	0.900
70.9	0.647	0.905
71.0	0.650	0.910
71.1	0.653	0.914
71.2	0.656	0.919

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
71.3	0.659	0.923
71.4	0.662	0.927
71.5	0.665	0.931
71.6	0.668	0.935
71.7	0.671	0.939
71.8	0.674	0.943
71.9	0.677	0.948
72.0	0.680	0.952
72.1	0.683	0.956
72.2	0.686	0.960
72.3	0.689	0.964
72.4	0.692	0.968
72.5	0.695	0.973
72.6	0.698	0.977
72.7	0.701	0.981
72.8	0.704	0.985
72.9	0.707	0.989
73.0	0.710	0.993
73.1	0.713	0.998
73.2	0.716	1.002
73.3	0.719	1.005
73.4	0.722	1.009
73.5	0.725	1.015
73.6	0.728	1.019
73.7	0.731	1.023
73.8	0.734	1.028
73.9	0.737	1.032
74.0	0.740	1.036
74.1	0.743	1.041
74.2	0.747	1.047
74.3	0.750	1.051
74.4	0.753	1.056
74.5	0.756	1.061
74.6	0.759	1.067
74.7	0.762	1.071
74.8	0.765	1.076
74.9	0.768	1.080
75.0	0.771	1.084
75.1	0.774	1.089
75.2	0.777	1.093
75.3	0.780	1.097
75.4	0.783	1.101

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
75.5	0.786	1.105
75.6	0.789	1.110
75.7	0.792	1.114
75.8	0.795	1.118
75.9	0.798	1.122
76.0	0.801	1.127
76.1	0.804	1.133
76.2	0.807	1.137
76.3	0.810	1.141
76.4	0.813	1.146
76.5	0.816	1.150
76.6	0.819	1.153
76.7	0.822	1.157
76.8	0.825	1.161
76.9	0.828	1.165
77.0	0.831	1.169
77.1	0.834	1.172
77.2	0.837	1.179
77.3	0.840	1.182
77.4	0.843	1.187
77.5	0.846	1.193
77.6	0.850	1.199
77.7	0.853	1.203
77.8	0.856	1.207
77.9	0.859	1.212
78.0	0.862	1.216
78.1	0.867	1.220
78.2	0.872	1.222
78.3	0.875	1.223
78.4	0.878	1.227
78.5	0.881	1.233
78.6	0.885	1.237
78.7	0.888	1.241
78.8	0.891	1.244
78.9	0.894	1.248
79.0	0.898	1.252
79.1	0.901	1.257
79.2	0.904	1.262
79.3	0.908	1.268
79.4	0.911	1.273
79.5	0.914	1.278
79.6	0.917	1.283

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
79.7	0.921	1.288
79.8	0.924	1.293
79.9	0.927	1.297
80.0	0.930	1.305
80.1	0.934	1.309
80.2	0.937	1.315
80.3	0.941	1.317
80.4	0.944	1.327
80.5	0.947	1.330
80.6	0.951	1.333
80.7	0.954	1.338
80.8	0.957	1.347
80.9	0.960	1.353
81.0	0.964	1.358
81.1	0.967	1.363
81.2	0.970	1.372
81.3	0.974	1.377
81.4	0.977	1.384
81.5	0.979	1.392
81.6	0.981	1.397
81.7	0.983	1.401
81.8	0.986	1.405
81.9	0.990	1.414
82.0	0.993	1.421
82.1	0.996	1.430
82.2	1.000	1.434
82.3	1.003	1.439
82.4	1.014	1.444
82.5	1.018	1.451
82.6	1.021	1.459
82.7	1.025	1.464
82.8	1.029	1.470
82.9	1.032	1.475
83.0	1.036	1.480
83.1	1.039	1.486
83.2	1.043	1.492
83.3	1.046	1.497
83.4	1.050	1.503
83.5	1.054	1.509
83.6	1.057	1.514
83.7	1.061	1.520
83.8	1.065	1.526

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
83.9	1.066	1.531
84.0	1.073	1.537
84.1	1.077	1.543
84.2	1.081	1.547
84.3	1.085	1.552
84.4	1.091	1.558
84.5	1.095	1.565
84.6	1.099	1.572
84.7	1.103	1.577
84.8	1.108	1.582
84.9	1.112	1.587
85.0	1.116	1.593
85.1	1.121	1.599
85.2	1.125	1.604
85.3	1.130	1.609
85.4	1.138	1.614
85.5	1.143	1.619
85.6	1.151	1.625
85.7	1.155	1.633
85.8	1.160	1.639
85.9	1.164	1.643
86.0	1.169	1.649
86.1	1.174	1.655
86.2	1.179	1.667
86.3	1.183	1.676
86.4	1.186	1.681
86.5	1.189	1.687
86.6	1.193	1.694
86.7	1.197	1.699
86.8	1.202	1.705
86.9	1.207	1.711
87.0	1.212	1.717
87.1	1.217	1.723
87.2	1.222	1.728
87.3	1.226	1.734
87.4	1.231	1.740
87.5	1.236	1.746
87.6	1.241	1.752
87.7	1.246	1.758
87.8	1.252	1.762
87.9	1.257	1.769
88.0	1.260	1.772

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
88.1	1.263	1.778
88.2	1.268	1.784
88.3	1.273	1.796
88.4	1.277	1.803
88.5	1.282	1.810
88.6	1.287	1.816
88.7	1.292	1.822
88.8	1.297	1.828
88.9	1.302	1.833
89.0	1.307	1.839
89.1	1.312	1.845
89.2	1.317	1.852
89.3	1.322	1.858
89.4	1.327	1.865
89.5	1.331	1.871
89.6	1.336	1.877
89.7	1.341	1.884
89.8	1.346	1.891
89.9	1.351	1.897
90.0	1.356	1.904
90.1	1.361	1.910
90.2	1.366	1.917
90.3	1.371	1.924
90.4	1.376	1.930
90.5	1.381	1.937
90.6	1.386	1.944
90.7	1.391	1.950
90.8	1.395	1.957
90.9	1.400	1.963
91.0	1.405	1.970
91.1	1.410	1.977
91.2	1.415	1.984
91.3	1.420	1.990
91.4	1.425	1.997
91.5	1.430	2.004
91.6	1.435	2.010
91.7	1.440	2.017
91.8	1.445	2.023
91.9	1.450	2.030
92.0	1.455	2.037
92.1	1.459	2.043
92.2	1.464	2.050

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
92.3	1.469	2.057
92.4	1.474	2.063
92.5	1.479	2.071
92.6	1.484	2.077
92.7	1.489	2.084
92.8	1.494	2.091
92.9	1.499	2.098
93.0	1.504	2.104
93.1	1.509	2.111
93.2	1.514	2.117
93.3	1.519	2.124
93.4	1.523	2.131
93.5	1.528	2.137
93.6	1.533	2.144
93.7	1.538	2.151
93.8	1.543	2.157
93.9	1.548	2.164
94.0	1.553	2.170
94.1	1.558	2.177
94.2	1.563	2.184
94.3	1.568	2.190
94.4	1.573	2.197
94.5	1.578	2.204
94.6	1.582	2.210
94.7	1.587	2.217
94.8	1.592	2.224
94.9	1.597	2.230
95.0	1.602	2.237
95.1	1.607	2.243
95.2	1.612	2.250
95.3	1.617	2.257
95.4	1.622	2.263
95.5	1.627	2.270
95.6	1.632	2.277
95.7	1.637	2.283
95.8	1.642	2.290
95.9	1.646	2.296
96.0	1.651	2.303
96.1	1.656	2.310
96.2	1.661	2.317
96.3	1.666	2.323
96.4	1.671	2.330

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
96.5	1.676	2.336
96.6	1.681	2.343
96.7	1.686	2.350
96.8	1.691	2.356
96.9	1.696	2.363
97.0	1.701	2.370
97.1	1.706	2.376
97.2	1.710	2.383
97.3	1.715	2.390
97.4	1.720	2.396
97.5	1.725	2.403
97.6	1.730	2.410
97.7	1.735	2.416
97.8	1.740	2.423
97.9	1.745	2.429
98.0	1.750	2.436
98.1	1.755	2.442
98.2	1.760	2.449
98.3	1.765	2.456
98.4	1.769	2.462
98.5	1.774	2.469
98.6	1.779	2.475
98.7	1.784	2.482
98.8	1.789	2.488
98.9	1.794	2.495
99.0	1.799	2.502
99.1	1.804	2.508
99.2	1.809	2.515
99.3	1.814	2.521
99.4	1.818	2.528
99.5	1.823	2.534
99.6	1.828	2.541
99.7	1.833	2.547
99.8	1.838	2.554
99.9	1.843	2.560
100.0	1.848	2.567
100.1	1.853	2.574
100.2	1.858	2.580
100.3	1.863	2.583
100.4	1.868	2.590
100.5	1.873	2.596
100.6	1.877	2.603

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
100.7	1.882	2.609
100.8	1.887	2.615
100.9	1.892	2.621
101.0	1.897	2.628
101.1	1.894	2.634
101.2	1.899	2.637
101.3	1.904	2.644
101.4	1.909	2.647
101.5	1.914	2.654
101.6	1.919	2.660
101.7	1.923	2.667
101.8	1.928	2.673
101.9	1.933	2.680
102.0	1.938	2.686
102.1	1.943	2.693
102.2	1.948	2.699
102.3	1.952	2.706
102.4	1.957	2.712
102.5	1.962	2.719
102.6	1.967	2.725
102.7	1.967	2.731
102.8	1.971	2.738
102.9	1.976	2.744
103.0	1.981	2.751
103.1	1.986	2.757
103.2	1.991	2.764
103.3	1.995	2.770
103.4	2.000	2.777
103.5	2.005	2.783
103.6	2.010	2.790
103.7	2.015	2.796
103.8	2.019	2.803
103.9	2.024	2.809
104.0	2.029	2.816
104.1	2.034	2.822
104.2	2.039	2.829
104.3	2.043	2.835
104.4	2.048	2.841
104.5	2.053	2.846
104.6	2.058	2.853
104.7	2.063	2.857
104.8	2.067	2.864

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
104.9	2.072	2.870
105.0	2.077	2.871
105.1	2.082	2.873
105.2	2.087	2.879
105.3	2.091	2.886
105.4	2.096	2.892
105.5	2.101	2.897
105.6	2.106	2.902
105.7	2.111	2.908
105.8	2.115	2.914
105.9	2.120	2.921
106.0	2.125	2.927
106.1	2.130	2.933
106.2	2.134	2.938
106.3	2.139	2.945
106.4	2.144	2.951
106.5	2.149	2.957
106.6	2.154	2.961
106.7	2.158	2.967
106.8	2.163	2.973
106.9	2.168	2.979
107.0	2.173	2.985
107.1	2.178	2.992
107.2	2.182	2.998
107.3	2.187	3.004
107.4	2.192	3.010
107.5	2.197	3.017
107.6	2.202	3.022
107.7	2.206	3.028
107.8	2.211	3.035
107.9	2.216	3.041
108.0	2.221	3.047
108.1	2.226	3.054
108.2	2.230	3.060
108.3	2.235	3.066
108.4	2.240	3.073
108.5	2.245	3.079
108.6	2.250	3.083
108.7	2.254	3.089
108.8	2.259	3.094
108.9	2.264	3.099
109.0	2.269	3.105

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
109.1	2.274	3.111
109.2	2.278	3.118
109.3	2.283	3.124
109.4	2.288	3.130
109.5	2.293	3.136
109.6	2.297	3.143
109.7	2.302	3.149
109.8	2.307	3.155
109.9	2.312	3.162
110.0	2.317	3.168
110.1	2.321	3.174
110.2	2.326	3.176
110.3	2.331	3.181
110.4	2.336	3.188
110.5	2.341	3.194
110.6	2.345	3.200
110.7	2.350	3.206
110.8	2.355	3.213
110.9	2.360	3.219
111.0	2.365	3.225
111.1	2.369	3.231
111.2	2.374	3.238
111.3	2.379	3.244
111.4	2.384	3.250
111.5	2.389	3.256
111.6	2.393	3.263
111.7	2.398	3.269
111.8	2.403	3.275
111.9	2.408	3.281
112.0	2.413	3.288
112.1	2.417	3.294
112.2	2.422	3.300
112.3	2.427	3.306
112.4	2.432	3.313
112.5	2.436	3.319
112.6	2.440	3.325
112.7	2.443	3.331
112.8	2.446	3.338
112.9	2.449	3.344
113.0	2.452	3.350
113.1	2.455	3.356
113.2	2.458	3.363

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
113.3	2.461	3.369
113.4	2.464	3.375
113.5	2.467	3.381
113.6	2.470	3.388
113.7	2.473	3.394
113.8	2.476	3.400
113.9	2.480	3.406
114.0	2.484	3.413
114.1	2.489	3.419
114.2	2.494	3.425
114.3	2.498	3.431
114.4	2.503	3.437
114.5	2.508	3.443
114.6	2.513	3.449
114.7	2.517	3.456
114.8	2.522	3.462
114.9	2.527	3.468
115.0	2.531	3.474
115.1	2.536	3.480
115.2	2.541	3.487
115.3	2.545	3.493
115.4	2.550	3.499
115.5	2.555	3.505
115.6	2.559	3.511
115.7	2.564	3.517
115.8	2.569	3.523
115.9	2.573	3.530
116.0	2.578	3.536
116.1	2.583	3.542
116.2	2.588	3.548
116.3	2.592	3.555
116.4	2.597	3.561
116.5	2.602	3.567
116.6	2.606	3.573
116.7	2.611	3.580
116.8	2.616	3.586
116.9	2.620	3.590
117.0	2.625	3.595
117.1	2.630	3.600
117.2	2.634	3.606
117.3	2.639	3.613
117.4	2.644	3.619

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
117.5	2.648	3.625
117.6	2.653	3.631
117.7	2.658	3.637
117.8	2.663	3.644
117.9	2.667	3.650
118.0	2.672	3.656
118.1	2.677	3.662
118.2	2.681	3.669
118.3	2.686	3.675
118.4	2.691	3.681
118.5	2.695	3.687
118.6	2.700	3.693
118.7	2.705	3.700
118.8	2.709	3.703
118.9	2.714	3.709
119.0	2.719	3.715
119.1	2.723	3.721
119.2	2.728	3.727
119.3	2.733	3.734
119.4	2.738	3.740
119.5	2.742	3.746
119.6	2.747	3.752
119.7	2.752	3.758
119.8	2.756	3.764
119.9	2.761	3.770
120.0	2.766	3.776
120.1	2.770	3.782
120.2	2.775	3.789
120.3	2.780	3.795
120.4	2.784	3.801
120.5	2.789	3.807
120.6	2.794	3.813
120.7	2.798	3.820
120.8	2.803	3.826
120.9	2.808	3.832
121.0	2.813	3.838
121.1	2.817	3.844
121.2	2.822	3.851
121.3	2.827	3.857
121.4	2.831	3.862
121.5	2.836	3.868
121.6	2.841	3.873

Chick head length (mm)	Body mass (kg) predicted at the 5% quantile	Body mass (kg) predicted at the 95% quantile
121.7	2.845	3.879
121.8	2.850	3.886
121.9	2.855	3.892
122.0	2.859	3.898