Factors impacting the breeding success of African penguins *Spheniscus demersus* on Robben Island

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is my own.

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Abstract

The African penguin *Spheniscus demersus* is a seabird endemic to the south-western coast of Africa and can be found in three main breeding localities; southern Namibia, the Western Cape and Algoa Bay, Eastern Cape, South Africa. The African penguin has been listed as Endangered since 2010, having experienced a decline in population of more than 50% over the past three generations.

This study was conducted at the breeding colony on Robben Island, South Africa, and examined two factors that have the potential to affect breeding success of African penguins; body mass at the onset of breeding and the suitability of various nest types to mitigate changing climatic conditions.

Body mass was measured by recording weights using an automated weighing scale set up in front of a nest. Weights were taken at the start of breeding of each penguin in a breeding pair and these weights were compared to the number of chicks fledged, fledging period, hatching success, clutch size, and chick fledging weight. Hatching success, clutch size, and fledging weight were not influenced by the mass of either parent. There was a trend of shorter fledging periods as the mass of the heavier parent increased. The greatest effect was from the body mass of the lighter parent on the number of chicks that fledged from the nest; as the mass of the lightest adult increased, more chicks were fledged. If the lighter adult weighed below 2 kg there were always no chicks at the nest that fledged. This suggests evidence for a carry-over effect of body mass from the time before breeding starts into the breeding season, and highlights the importance of food availability for African penguins on a global scale, and not just a local one.

The proportion of nest failures of six nest types (vegetation, open, natural burrow, building, wooden nest box, and artificial fibreglass burrow) at the incubation and chick-rearing stage were compared to rainfall and maximum temperature. At incubation, nest failure was lower in nest boxes than in open and vegetation nests. Incubation failure increased with rainfall, but only increased with temperature based on nest type. Nest failure decreased in nest boxes as temperatures increases, whereas nest failure increased in all other nest types. During chick-rearing, nest failure was lower in nest boxes and artificial burrows than in natural burrows, open and vegetation nests. Chick mortality increased with both rainfall and temperature.

When artificial burrows were analysed rainfall no longer had an effect on nest failure at the incubation and chick-rearing stage.

Operative temperatures were measured inside nest boxes, artificial burrows, under vegetation, and on the surface. Artificial burrows and nest boxes were cooler than nests on the surface, with artificial burrows being slightly cooler than nest boxes. Vegetation nests, however, had lower and more stable temperatures,, and had fewer temperatures above 30°C than all other nest types.. Nest boxes placed at different orientations had variations in the amount of time internal temperatures exceeded 30°C.

Artificial nests did not increase nesting failure and can be used as substitute nesting habitat for African penguins, but the current designs are not optimal because they are hotter than nests in natural vegetation. Long-term temperature data from Robben Island showed an increase in the number of days experiencing high temperatures during the first three months of the African penguin breeding season, and so further research on the design of artificial nests will benefit the conservation of African penguins.

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Chapter 1

Introduction:

Background information on seabird body condition, climate variability, nesting habitat, Robben Island and the African penguin

Seabirds and body condition

Seabirds are long-lived, and to maximize their fitness, they have to weigh the trade-offs of current versus future reproduction (Harding *et al.* 2009). Body condition can influence the decision of a seabird to allocate food to its offspring or to build up its own energy reserves for survival (Weimerskirch *et al.* 1997). When breeding Antarctic petrels *Thalassoica antarctica* had low body mass they would be more likely to prioritize their own energy requirements before the chicks' (Varpe *et al.* 2004). Thus poor body condition could negatively affect the breeding success of seabirds. For example, Adélie penguins *Pygoscelis adeliae* in poor condition prioritized self-maintenance by delivering less food to their chicks, resulting in chicks with a lower fledging mass (Ballard *et al.* 2010). On the other hand, Antarctic petrels in good body condition had a greater chance of having a chick survive past 8 days after hatching, and those chicks were also heavier (Tveraa *et al.* 1998).

Body condition of a seabird before rather than just throughout breeding may also influence breeding success. If a breeding seabird builds up reserves, they may carry over into the subsequent breeding season and positively affect offspring survival. These reserves may also influence the decision of whether or not to breed. Weimerskirch (1992) found that if the body mass of a female wandering albatross *Diomedea exulans* was below a certain mass threshold they postponed the first breeding attempt, and a study of blue petrels *Halobaena caerulea* determined that body condition of both males and females influenced the decision to breed (Chastel *et al.* 1995b). Salton *et al.* (2015) studied little penguins *Eudyptula minor* and found that males and females with a greater body mass during the non-breeding season were more likely to start breeding early, and males with a greater body mass were likely to have a successful breeding attempt. Crawford *et al.* (2008) reported that mass at arrival for male and female rockhopper penguins *Eudyptes chrysocome* significantly correlated with breeding success. On the other hand, poor adult body condition at onset of breeding can result in the abandonment of nests during the incubation period (Chastel *et al.* 1995a, Yorio and Boersma 1994). It is likely that if adults fall below a certain mass threshold, the result would be nest abandonment or failure to start breeding (Chastel *et al.* 1995a, Chaurand and Weimerskirch 1994). Yorio and Boersma (1994) reported that Magellanic penguins *Spheniscus magellanicus* that abandoned were lighter for their size at time of egg-laying, compared to those that did not abandon. In the blue petrel, poor body condition resulted in a lower chance of an egg hatching or a chick fledging (Chastel *et al.* 1995a).

Body condition can serve as a proxy for the availability of food before and during the breeding season (Salton *et al.* 2015). Food availability must be adequate to ensure good body condition and successful breeding (Clarke 2001). Sherley *et al.* (2013) hypothesised that the regional abundance of prey was linked to adult condition prior to breeding in African penguins *Spheniscus demersus*. Food availability before the start of breeding could thus be important for allowing the storing of energy reserves for breeding, which would help buffer any changes in local food availability during breeding. If local conditions are good, then an adult in good body condition at the start of breeding can use more energy for the provisioning of the chicks, rather than for its own condition (Sherley *et al.* 2013). If local feeding conditions are poor, good body condition at the start of breeding might not be enough for adults to maintain body condition and successfully raise their chicks (Sherley *et al.* 2013, Suryan *et al.* 2002).

Measuring body condition

Fat content accurately represents energy reserves and body condition (Jacobs *et al.* 2012, Labocha and Hayes 2012, Schamber *et al.* 2009). A variation in body condition can be associated with a variation in fat content, but body fat can only be directly measured through dissection (Schamber *et al.* 2009). For non-lethal measures, body mass was a good predictor of total body fat content for species with a high percentage of fat (Jacobs *et al.* 2012). Body mass and fat mass can be correlated if birds are similar in structural size, gut content mass, hydration and organ and muscle mass (Labocha and Hayes 2012).

Many studies use body mass as a measure of condition (e.g. Ballard *et al.* 2010, Salton *et al.* 2015, Vleck and Vleck 2002). Body mass is relatively easy to measure in the field, repeatable, and often explains over 50% of variation in body fat (Labocha and Hayes 2012).

The size of the bird also matters in body condition because a larger bird, depending on its percent of body fat, could be in better or worse condition than a smaller bird. This makes it difficult to make any real conclusions based on body mass alone (Labocha and Hayes 2012).

In many other cases, a body condition index is determined by scaling body mass with body size (Chastel *et al.* 1995a), to account for the effect of body size on body mass (Golet *et al.* 1998), and more accurately represent fat stores (Peig and Green 2009, 2010)**.** The structural measurements used in developing an index vary depending on the study. Examples of some of the size measurements used are: head-bill length (Golet and Irons 1999), flipper length (Numata *et al.* 2000, Robinson *et al.* 2005), culmen length (Chastel *et al.* 1995b), and bill depth (Erikstad *et al.* 1997). Some studies used a collection of measurements to perform a principle component analysis (PCA) to determine an index of body size (e.g. Chastel *et al.* 1995b, Erikstad *et al.* 1997, Yorio and Boersma 1994), and some found one measurement to correlate best to body mass (e.g. Jakubas *et al.* 2011, Numata *et al.* 2000, Robinson *et al.* 2005). Schamber *et al.* (2009) stresses the importance of choosing the right structural measurement for a condition index because measurements, when related to body mass, can vary in correlation with fat mass, and subjectively selecting an index can result in a loss of precision, and the same condition index may not be applicable for all species or even sexes (Schamber *et al.* 2009).

Seabirds and climate variability

Climate change has resulted in changes in extreme weather events globally since ca. 1950. Cold temperature extremes are decreasing while hot temperature extremes are increasing, and heavy rainfall events have increased in certain regions. Surface temperatures in the last three decades have been warmer than any previous decade since 1850, increasing by 0.85°C (IPCC 2014).These trends are only expected to continue. Models suggest that the global mean surface temperatures will increase by 2050, compared to 1961–1990 (Rowlands *et al.* 2012), and are likely to increase by 1.5°C by the end of the 21st century. This would result in an increase in the frequency of higher temperatures and heat waves (IPCC 2014).

The effects of climate change could have a significant impact on seabird populations (Crick 2004). They can lead to the mortality of exposed eggs and chicks (Boersma and Rebstock 2014, Sherley *et al.* 2012a), and this can impact future recruitment as fewer chicks will fledge

(Boersma and Rebstock 2014). Climate change and changing oceanic conditions could also impact the availability of food, affecting adult condition and survival, timing of breeding, and breeding success (Forcada and Trathan 2009). For example, an El Niño event, reducting nutrient rich waters, resulted in total nest failure of a Galápagos penguin colony (Boersma 1998). When prey is scarce, seabird adults are unable to find enough food to provision their chicks properly or they may abandon the nest (Frere *et al.* 1998).

Heat

Seabirds are endothermic; they have a range of temperatures where the amount of energy expended for thermoregulation is low called the thermal neutral zone. If temperatures fall outside these limits, seabirds must use more energy through thermoregulation to maintain thermal homeostasis (Oswald and Arnold 2012). Seabirds thermoregulate near their upper temperature limit. If they are exposed to temperatures above this limit, they are likely to become heat stressed. Exposure is not just from air temperatures; metabolic heat production and solar radiation must also be taken into consideration (Oswald and Arnold 2012). Many species of seabirds, breeding in nests on the surface or in low-lying vegetation are exposed to increased heat loads from solar radiation (Frost *et al.* 1976a, Randall 1983).

Seabirds will adopt various morphological, physiological, and behavioural responses to maintain thermal homeostasis (Lustick 1984). Throughout breeding they are unable to leave the nest while the partner is foraging. This means that they must increase thermoregulatory behaviours, such as panting, to avoid overheating (Frost *et al.* 1976a). They will also adjust body posture and orientation to reduce heat gain (Randall 1983, Frost *et al.* 1976a). African penguins have been observed orientating towards the sun on hot days (Randall 1983) to reduce the exposure of their black plumage. This is because dark plumage has lower reflectance than white plumage (Randall 1983) and can increase the heat loads on birds (Lustick 1984). Seddon and Davis (1989) observed an increase in panting and restless movements in yellow-eyed penguins *Megadyptes antipodes* as temperatures increased. Evaporative cooling by means of panting or gular flutter is an effective form of heat loss but can cause osmotic stress and seabirds might have to temporarily leave the nest to drink (Oswald and Arnold 2012). If these thermoregulatory methods are unsuccessful at reducing heat gain, a bird's final resort is to abandon the nest (Randall 1983).

Extreme heat can thus have a negative impact on breeding seabirds. Barham *et al.* (2007) reported that excessive heat caused the abandonment of a large number of African penguin nests on Robben Island. Periods of high temperatures resulted in the mortality of bank cormorant *Phalacrocorax neglectus* chicks (Sherley *et al.* 2012a), and African penguins in Namibia experienced a windless day where the maximum temperature hit an extreme that resulted in the mass abandonment of 87 nests and the death of 68 chicks (Kemper *et al.* 2007a). Rather than general warming, it seems that a heat wave over a period of one or two days can be enough to cause lasting damage. Salzman (1982) recorded a heat wave with little wind in a western gull *Larus occidentalis* colony, and the next day discovered the mass mortality of gull chicks, with the percentage of mortality varying throughout the colony. A later study found that nests in areas of higher mortality recorded higher air temperatures, lower wind velocities, and higher operative environmental temperatures then those nests in the low mortality areas, and that mortality was not related to vegetation cover (Salzman 1982).

Chicks can suffer from overheating if they are not in a well-shaded area (Seddon and Davis 1989). Younger chicks are especially vulnerable to hyperthermia because they are still covered in down, as was found to be the case with Adélie penguin chicks (Chappell *et al.* 1990). Stokes and Boersma (1998) recorded the largest number of Magellanic penguin chick mortalities during the hottest days. Even if increased temperature does not cause death, it could have a negative effect on mass gain as chicks may need to spend more of their energy on thermoregulation (Cunningham *et al.* 2013).

Rain and storm events

Stormy weather, such as heavy rain, wind, and extreme cold temperatures can have a detrimental effect on the breeding success of seabirds. A storm event caused flooding of a large number of African penguin nests (Barham *et al.* 2007). Poor breeding success for a bank cormorant colony was the result of two big storm events that occurred during peak breeding (Sherley *et al.* 2012a). An intense storm at an African penguin colony resulted in flooded burrows, washed away eggs, drowned chicks and deaths due to hypothermia (de Villiers 2002) and two storm events that occurred in two different years resulted in the death of over 50% of Magellanic penguin chicks (Boersma and Rebstock 2014).

Heavy rains can fill up and flood nests, and these were more likely to be abandoned (Yorio and Boersma 1994). Nest flooding can also result in direct chick mortality (Frere *et al.* 1998, Stokes and Boersma 1991, 1998). Not only can storms cause flooding, but they can also cause the collapse of burrows (Yorio and Boersma 1994) or the complete loss of nests (Sherley *et al.* 2012a).

Rain coupled with cold temperatures can result in hypothermia for a chick that still has down; if they get wet they lose heat more quickly (Boersma and Rebstock 2014), and cold temperatures require the need for more energy expenditure on thermoregulation (Crick 2004). As the chicks get older they are at less of a risk as they would have started to develop waterproof plumage, and chicks younger than 9 days are still provided complete cover by the parent through brooding (Boersma and Rebstock 2014).

Nest types and breeding success

Breeding success can vary depending on nesting habitat.. Eggs and small chicks are most vulnerable to predation (Frere *et al.* 1992), nest flooding, exposure, and abandonment (Sherley *et al.* 2012b). Larger chicks are most affected by starvation and heat stress (Kemper *et al.* 2007b). Before chicks are able to defend themselves, they rely on good nest cover and the protection of the parents (Salzman 1982). Nests with adequate cover influence the survival of penguins. They have been found to have fewer mortalities (Demongin *et al.* 2010, Seddon and van Heezik 1991), less abandonment (Sherley *et al.* 2012b), higher fledging success (Stokes and Boersma 1998), and overall, nests with cover demonstrated greater breeding success then exposed nests (Kemper *et al.* 2007a). Burrows, the historic nesting habitat for African penguins, provide the necessary cover, but if they collapse, young chicks may die through smothering or by being crushed by the adult (Seddon and van Heezik 1991).

Nests must have proper cover and insulation to protect against extreme temperatures. Thermoregulatory behaviours seemed to decrease when there was a greater amount of cover over the nest (Seddon and Davis 1989). Natural burrows, if well insulated, also protected from high temperatures (Dann and Chambers 2013, Lei *et al.* 2014) because they provide a constant microclimate (Frost *et al.* 1976a). Surface nests with no or little cover experience hotter temperatures compared to nests with greater cover (Stokes and Boersma 1998), and are more likely to fail (Kemper *et al.* 2007a). There is also a greater risk of chicks in open nests leaving the nest at a younger age to find a more shaded area, which could make them more vulnerable (Stokes and Boersma 1998). The amount of nest cover can also be crucial in protecting against stormy weather; open nests expose chicks to rain and wind which could cause hypothermia (Seddon and van Heezik 1991).

Artificial Nests

Artificial nests provide alternative breeding habitat for seabirds (Kemper *et al.* 2007a, Pichegru 2013, Ropert-Coudert *et al.* 2004, Sherley *et al.* 2012b), and they have been shown to improve breeding success in many cases. Sherley *et al.* (2012b) found African penguins on Robben Island that occupied artificial nests were the most successful; fledging more chicks than those in vegetation nests. This is probably because of their ability to protect against predation and heat stress. They would also not be vulnerable to collapse or flooding. Kemper *et al.* (2007a) also found African penguins in artificial burrows showed fewer signs of heat stress when it was a hot day, compared to those in surface nests, and reported overall improved breeding success with artificial nests. Successful use of artificial nests is likely site-specific and dependent on their design (Pichegru 2013). Pichegru (2013) found that artificial fibreglass burrows had lower African penguin hatching success compared to artificial cement pipe nests. Catry *et al.* (2011) reported greater chick mortality and poorer body condition of lesser kestrels *Falco naumanni* due to high temperatures experienced inside nest boxes. The temperature experienced inside artificial nests may be an important factor in their success. Wooden nest boxes with poor ventilation recorded temperatures greater than outside air temperatures (Catry *et al.* 2011, Ropert-Coudert *et al.* 2004) and Lei *et al.* (2014) found that artificial nests, especially fibreglass burrows, experienced higher temperatures than natural burrow nests, suggesting that the design did not perfectly mimic the microclimate of a natural burrow.

The placement of artificial nests could also have an effect on conditions inside them. Tree swallows *Tachycineta bicolor* demonstrated a preference for nest orientation only during warmer temperatures, which could indicate that they will choose a nest box based on temperature. South and east-facing nest boxes warmed up faster in the morning and the birds might favour these rather than the ones that are cooler, and by the afternoon there was no difference in temperature (Ardia *et al.* 2006). West-facing nest boxes recorded lower average temperatures compared to south or east-facing boxes, and there was lower hatching success for American ketrels *Falco sparverius* in southwest-facing nest boxes (Butler *et al.* 2009). Catry *et al.* (2011) reported no chick mortality in nest boxes facing north compared to other orientations and the north facing nest boxes had the coolest temperatures. Frere *et al.* (1992)

suspected that orientation doesn’t have a large effect and rather the design and topography around the nests make the difference.

Study species: The African penguin

The African penguin is endemic to southern Africa. It is part of the Benguela upwelling ecosystem (Crawford *et al.* 2011), and is the only penguin that breeds on the continent of Africa (du Toit *et al.* 2003). In South Africa and Namibia, African penguins have been found breeding at 28 colonies, mostly islands. Vagrants have been found much further north, on the east and west coasts; Gabon and Inhaca Island, Mozambique respectively (du Toit *et al.* 2003). The three main breeding localities are located in southern Namibia, the Western Cape and in Algoa Bay, in the Eastern Cape, South Africa.

African penguin breeding is not always synchronous. In South Africa, the majority breed during the austral winter, whereas in Namibia they can be found breeding during the summer months. On Robben Island, 34% of clutches were laid in February and 94% were laid by the end of May (Crawford *et al.* 1999). Adult African penguins generally start breeding between 4 to 5 years of age (Whittington *et al.* 2005). They show high fidelity to colonies and mates, with some nest site fidelity (Randall 1983). Clutches of one to two eggs are laid (Crawford *et al.* 1999) and incubated equally between the pair for 38–41 days (Hockey *et al.* 2005). Once chicks are hatched they are provisioned by both parents and generally fledge after 75–80 days (Seddon and van Heezik 1993). Breeding adults mostly forage within 20 km of the breeding colony, with trips usually lasting less than 24 hours (Wilson *et al.* 1988).

African penguins are listed as Endangered (IUCN 2014), and have declined in population by at least 90% during the 20th century (Crawford *et al.* 2001, du Toit *et al.* 2004). The number of breeding African penguins was around 48 000 pairs from 1979 to 2004. Numbers then experienced a rapid decline and in 2013 the population has fallen to 17 000 pairs. In the Western Cape, the population decreased by over 75% between the years 2001 and 2013 (Crawford *et al.* 2014).

The decline in numbers in the early 20th century is thought to be caused by the over-harvesting of eggs and guano. Penguin eggs were collected for human consumption and layers of guano were removed from breeding grounds for use as a fertilizer, causing disturbance and destruction of habitat (Frost *et al.* 1976b). The diet of the African penguin consists mostly of anchovy *Engraulis encrasicolus* and sardine *Sardinops* sagax (Hockey *et al.* 2005). Since the 1950's, they have had to compete with commercial fisheries for prey resources (du Toit *et al.* 2004). These prey species have also experienced an eastward shift in their distributions, potentially due to changes in environmental conditions (Roy *et al.* 2007), which led to a mismatch in prey distribution and penguin breeding localities (Crawford *et al.* 2011). Other factors that threaten population numbers of African penguins include predation (e.g. Kelp Gulls *Larus dominicanus* and Cape fur seals *Arctocephalus pusillus*; Pichegru 2013, Crawford *et al.* 2001), oiling (Wolfaardt *et al.* 2008, 2009), and competition for breeding space (Hockey *et al.* 2005).

Study site: Robben Island

Robben Island (33°48' S, 18 22' °E) is located in Table Bay, 11 km north of Cape Town and 7 km from Bloubergstrand; the nearest mainland. It is the largest of the islands along the south-western coast of Africa, with an area of 507 ha (Crawford and Dyer 2000). Similar to the mainland, the island experiences a temperate, Mediterranean climate. The summer months are usually warm and dry and the winter months cold and wet (Sherley 2010). Mean maximum temperature is usually highest in the month of February, and rainfall is usually highest in June (South African Weather Service, unpubl. data).

The island has a long history of human activity; it has been used for agriculture and the exploitation of seabirds and seals; it was home to lepers, the mentally ill, and prisoners (Crawford and Dyer 2000); it was run as a military establishment and as a maximum security prison. This activity has resulted in a significant change from its original state through the introduction of alien plant and animal species (Robben Island Museum 2013), and because of this the island is covered by exotic vegetation such as rooikrans *Acacia Cyclops*, manatoka *Myoporum serratum* and various *Eucalyptus*. It is also home to various animal species that had been introduced in the past, such as the European rabbit *Oryctolagus cuniculus*, feral cats *Felis catus*, and fallow deer *Dama dama* (Crawford and Dyer 2000).

Robben Island was declared a World Heritage Site in 1999 because of its cultural significance (Robben Island Museum 2013). It has also been identified as an Important Bird Area in South Africa (Barnes 1998). The island provides valuable breeding habitat for many seabird species, including three endangered species; the African penguin, the Cape cormorant *Phalacrocorax capensis* and the bank cormorant.

African penguins were first recorded breeding on the island as early as 1620, but stopped breeding about two centuries ago (Crawford *et al.* 1995), due to over exploitation and disturbance by humans (Crawford and Dyer 2000). They recolonized the island in 1983 (Crawford *et al.* 1995) and the colony grew from nine breeding pairs to become the third largest colony overall with just over 8500 pairs by 2004. However, the number of breeding pairs started to rapidly decline resulting in an estimate of only ca. 1200 pairs on the island in 2013 (Weller *et al.* 2014).

Study objective

I examined two factors impacting breeding success of African penguins on Robben Island: body mass at onset of breeding and nest type relating to climate. The first chapter focuses on the effect of body mass at the onset of breeding of individuals in a pair. Body condition at onset of breeding may be important in determining breeding success, while food availability prior to breeding may be linked to body condition at the start of breeding (Sherley *et al.* 2013). A non-invasive method is used to weigh adult penguins at the nest either while still prospecting or within a few days of egg-laying. These data are then compared to various breeding parameters to determine whether there is a carry-over effect of body mass at the start of breeding on subsequent breeding success, which could indicate the importance of adequate resources outside the breeding season as well as during the season.

The second chapter focuses on the differences between nest types and how suitable they are at mitigating climatic effects. Long-term data on nest failure for various nest types is compared to weather events to determine if there are any effects based on nest type. Operative nest temperatures are recorded to get an idea of which nest type is most optimal at protecting breeding penguins from exposure to high temperatures that could lead to nest failures.

Chapter 2

Body mass of adult African penguins at the onset of breeding and the effect on breeding success

Abstract

African penguin numbers have been experiencing a rapid decline in the past three decades, resulting in a classification of Endangered by the IUCN Red List. Body condition throughout breeding affects breeding success, but it has been thought that condition prior to breeding may carry over and also have an impact on breeding success. This study collected weights of adult African penguins at the onset of breeding for two breeding seasons, using an automated weighing scale to minimize disturbance. The body mass of individuals in a pair were then compared to various breeding parameters such as number of chicks fledged, fledging period, hatching success, clutch size, and chick fledging weight. Body mass, particularly of the lighter adult, had a positive effect on the number of chicks fledged. These findings provide some evidence of a carry-over effect of body mass on subsequent breeding. African penguins rely on adequate food availability throughout the breeding season, which can be linked to body condition. This could demonstrate the importance of adequate food resources not just during breeding but also during the non-breeding season to allow for the build-up of reserves.

Introduction

Seabirds are long-lived and have low fecundity which means any costs to their survival could affect their life-time reproductive success (Williams *et al.* 2007). Throughout a breeding attempt, birds face a constant trade-off in deciding how much energy to invest in reproduction and self-maintenance (Tveraa *et al.* 1998).

An adequate energy reserve throughout breeding is vital for the successful rearing of chicks. If these reserves are too low, long-lived seabirds will prioritize self-maintenance and their own survival, rather than focusing on reproduction (Drent and Daan 1980). The amount of parental investment into breeding preparations, such as the accumulation of energy reserves from food resources, may thus improve offspring survival (Salton *et al.* 2015).

Food availability provides the energy required for chick-rearing, but it can vary throughout the breeding season (Hamer *et al.* 2002) and may not always meet a bird's energy requirements. If breeding parents build up energy reserves before the onset of breeding, they may be able to buffer any changes in food availability throughout the breeding season and be able to maintain their own reserves while still providing for their chicks (Chastel *et al.* 1995a, Robinson *et al.* 2005, Salton *et al.* 2015). When these energy reserves are combined with abundant local prey availability during breeding, breeding parents would be better able to balance the trade-off between self-maintenance and chick provisioning, and so provide more resources to their growing chicks (Ballard *et al.* 2010, Sherley *et al.* 2013).

Body condition can be used as a proxy for food availability that reflects conditions prior to and during breeding (Salton *et al.* 2015). Studies have linked body condition to breeding success and even the decision to breed in several seabird species. For example, little penguin body condition during breeding has been linked to timing of breeding, breeding success, and foraging behaviour (Robinson *et al.* 2005). In blue petrels, early body condition influenced the decision to breed (Chastel *et al.* 1995a). Poor body condition at the start of the breeding season could also result in abandonment of nests during incubation (Chastel *et al.* 1995a, Yorio and Boersma 1994).

Body condition at the onset of breeding may thus determine reproductive success, but studies demonstrating this are scarce in seabirds that forage in coastal waters and do not undertake prolonged periods of migration (resident species; Salton *et al.* 2015). This could be especially true for seabirds that are capital breeders, such as the blue petrel (Chastel *et al.* 1995a), who accumulate their energy reserves before breeding, rather than income breeders, who accumulate their reserves gradually throughout breeding. Income breeding is less energetically costly and may be considered the better option when local food resources are reliable and abundant. However, capital breeding can be beneficial in unpredictable environments where food availability can be very variable (Jönsson 1997). Salton *et al.* (2015) speculates that many species actually adopt a combination of capital breeding and income breeding instead of solely relying on one or the other.

African penguins are listed as an endangered species (IUCN 2014) and a reduced availability of prey is considered to be one of the reasons for their drastic decline in recent years (Crawford *et al.* 2011, 2014). African penguins rely on adequate local food resources throughout the breeding season, but they also rely on regional food availability during the non-breeding season for their survival and to build up body reserves (Sherley *et al.* 2013, 2014). Sherley *et al.* (2013) found that when food availability (sardine biomass) prior to the breeding season was low, fledging periods for African penguins were longer, suggesting that regional food resources, which could be reflected by body condition at the onset of breeding, could be an important link in determining breeding success.

There is not much data on the condition of African penguins prior to the start of breeding mostly because of difficulties collecting these data (Sherley *et al.* 2013). For this chapter, I obtained weights of adult African penguins just before or at the start of breeding from each bird in a breeding pair using automated weighing scales placed at individual nest sites. The goals for this chapter were to develop a minimally-invasive method to determine the effect of body condition at the onset of breeding on breeding success by comparing weights obtained at the start of breeding from each bird at the nest to the number of chicks fledged, the number of days between hatching and fledging (fledging period), hatching success, clutch size, and chick fledging weight.

I predicted that adults with a greater body mass would fledge more chicks per nest; I also predicted that birds with a larger body mass would fledge their chicks over a shorter time, and that heavier parents would also produce a heavier chick at the time of fledging, because they would not have to focus as much on self-maintenance and would be able to provide more food to their chicks (Tveraa *et al.* 1998). Salton *et al.* (2015) found evidence that body mass of little penguins accumulated in the non-breeding season carried over to the start of the breeding season and had a positive effect on breeding success. It is possible that the body mass of just one of the adults may produce a greater effect than the combined body mass, so I analysed the weights separately and together. For example, if one partner has a low body mass the other partner may need to compensate, and this could negatively affect the success of the nest (Harding *et al.* 2009).

Materials and Methods

Data Collection

Development and design of the automated weighing scales and the associated electronics were part of student projects in the Department of Physics at the University of Bristol; these scales were specifically designed for use in African penguin research. The focus of the design was to ensure that weights could be recorded with minimal disturbance to the penguin. Human presence is only required at initial set up, and to change batteries or retrieve data. At no point do the penguins need to be handled as the weights are recorded automatically and stored for later retrieval (Pickering 2012, Young 2012).

The scales used were PS-105 Parcel Scales measuring 30 cm x 30 cm, connected to EHI-B weighing indicators (Figure 2.1). These had a 60 kg weight limit and an accuracy of ±0.1 kg. The microprocessor used was an Amicus18 board and this was programmed using the proton BASIC language. The Amicus18 accomplishes the functions required to perform and record measurements, and saves them for later analysis. This eliminates the need for a PC to be nearby, allowing the scale to be set up within the penguin colony. The scales had an RS-232 interface for serial communication between the scales and the Amicus18, which allowed data to be transmitted to the Amicus18 whenever it was created by the scales (see extended details; Pickering 2012, Young 2012).

Each scale was connected to an IP66 waterproof box containing a data logger and batteries (Figure 2.1). The scale was then placed into a waterproof and airtight 35 L dry bag to protect the electronics from environmental conditions. A square cut piece of flat wood was used as a base underneath the legs of the scale to aid with balance and levelling. The scale was manufactured so that it does not have to be perfectly level to get a proper reading. The box does not have to be level and was placed so as not to interfere with the penguins entering or exciting the nest. The ground in front of a nest was dug up to fit the scale, making sure the scale sat at roughly the same height as the ground so as to prevent as much obstruction to the birds as possible, but still ensuring that the penguins had to walk or stand on it as they entered or exited the nest. This was accomplished by putting it as close to the nest entrance as possible. Dirt and foliage were used to camouflage the scale (Figure 2.2).

The scale required six D-cell alkaline batteries to operate both the data logger and the scale, and the batteries typically lasted up to a maximum of 8 days. A micro SD card (2GB or 4GB) recorded weight readings in kilograms along with an error log in the form of a .csv file, including the date and time. A weight reading was logged every four seconds. The main on and off switch was located on the outside of the box, but the scale itself had to be turned on from within. This was usually done once the scale was already placed in the field. The batteries and SD card could be changed as needed with the scale *in situ*, causing a minimum amount of disturbance.

Bushnell® HD Trophy Cam™ camera traps were secured opposite the nest site (Figure 2.2) to record the penguins' movements in front of the nest. A penguin would walk over or stand on the scale and the movement would trigger the camera trap to take a picture. The pictures allowed me to identify the individual penguin in the breeding pair, and attribute a specific weight to a specific penguin. A penguin was identified by the spot pattern (Sherley *et al.* 2010), the plumage pattern under the flipper, the presence or absence of a tail spot, and at two of the nests one of the individuals from a pair was flipper banded. Both photographs and videos were experimented with, and it was found that video was easier for the identification of birds without any distinct markings or bands.

The camera traps captured infrared images and video that were stored onto an SD memory card and the date and time were set to coordinate with the scale's data logger. The camera traps were placed so that there was a clear view of the scale and the penguin when it was standing on the scale. The camera traps contained a motion sensor and were set to only trigger when movement was detected. The cameras were set to capture three consecutive photos or record 20 seconds of video when it was triggered, with a three second delay between sets. The camera traps included an Infrared flash for image capture after dark, but the flash had to be partially covered with tape to prevent whiteout of the penguins in the image.

Weights were chosen when it was clear that the individual was standing directly on the scale. All four second weight readings, within a time scale of four seconds to at most one hour, were averaged to obtain one mean weight for each bird. Weight readings were only considered if camera imagery could confirm the presence of a penguin on the scale. If there was a large fluctuation in weight between readings then the data was ignored as it likely meant that a bird was moving too much to allow an accurate reading and may not have been standing completely on the scale. Likewise, unusually large and small weights were not used if it could not be confirmed that one penguin was standing directly on the scale. In many cases, it was possible to observe if both birds were standing or lying on the scale, or if a bird was only partially on it (e.g. only one foot on the scale).

I used body mass (weight) as an index of body condition and did not control for size. Adults were not handled so no linear measurements, such as head length, could be taken. The scale was put in place so that weights could be recorded without the need to handle the bird, allowing for the minimal amount of disturbance. There are many studies where body mass alone is used as a measure of condition (Ballard *et al.* 2010, Salton *et al.* 201, Vleck and

Vleck 2002). Labocha and Hayes (2012) state that body mass can be a reasonable indicator of body condition, and one that is easy to measure.

Nest Selection

Nests where adults were defending sites prior to breeding (prospecting) were chosen and monitored to determine whether or not the female would lay eggs. A scale was placed in front of the nest either during prospecting or just after an egg had been laid in order to obtain a mass measurement from both adults at the onset of breeding. The scale was left out for two days and then the data was checked to see if the pair had changed over. If this was not the case, the scale was put out for another two to three days to ensure a mass measurement was obtained. Photos and video from the camera showed in many cases that during incubation, one partner would stay out between two to four days before returning to the nest to switch incubation duties. Randall (1983) reported that incubation shifts of five days were common and even reported some over 7 days. Once data were collected for both adults, the scale was removed and placed at new potential nest.

Breeding success

I visited each study nest every 5 to 10 days after measuring a pairs' weights to obtain an approximate hatching date and an approximate fledging date. After hatching, I recorded the number and size of the chicks following Barham *et al.* (2007). Chick size was recorded based on a classification scale (Barham *et al.* 2007); P0: newly hatched, eyes unopened. P1: eyes open, sitting under parent. P2: sitting independent of parent, completely downy. P3: partial loss of down. P4: over 50% of body has lost down. A nest was considered to have fledged successfully if the chicks reached the P4 stage (Sherley 2010, Barham *et al.* 2007), and monitoring continued until the nest was found to be empty. Breeding success is likely overestimated since an empty nest does not necessarily mean the chick has fledged; chicks may have just moved further away from the nest, or they could have joined a crèche and could no longer be identified as the ones belonging to a specific nest (Sherley *et al.* 2012b). There is also a chance that even though they reached P4 stage they were not fit enough to survive after leaving the nest (Kemper *et al.* 2007b)

Fledging weights were taken at each of the study nests. Once the chicks reached late P3 and P4 stage a mass measurement was taken of each chick at the nest, using a digital scale with a precision of at least 0.01 kg, every 5–7 days until the chicks were no longer found at the nest and were assumed to have fledged.

Fledging period was also determined for each nest; following Barham *et al.* (2007), it was recorded when a chick was first seen and when it was last seen at the nest. The difference between these two dates would determine the fledging period. Checks, however, may not pick up the exact hatching date of the chick and a recorded fledging date estimate of less than 60 days may be because chicks moved further away from the nest or joined a crèche (Sherley *et al.* 2012b), resulting in an underestimate of the fledging period (Sherley *et al.* 2013).

Data analysis

All data were analysed with linear regression models using the lm function from the stats package in R v. 3.1.2 (R Core Team 2014). Various aspects of breeding success were used as the response variables: number of chicks fledged (nest outcome), fledging period, fledging weight, hatching success, and clutch size. A mass, year interaction was used as the fixed effect.

The weights of the heavier adults from each nest were grouped together and the same was done with the lighter adults. These two groups and mean body mass of the pair were compared separately to the response variables. I looked at individual mass to see whether just one adult in a pair could have an effect on breeding success, since these effects may not be apparent if mass is combined.

Nest outcome was reported as 0, 1, or 2 chicks fledged. Fledging period was analysed to include any outliers (fledging periods of < 60 days) and was then analysed to exclude these outliers as the usual fledging period is 75–80 days (Seddon and van Heezik 1993). Hatching success was determined as a proportion (0, 0.5, and 1) of the number of eggs hatched from the number of eggs laid.

A generalized linear model (GLM) with a binomial error distribution and a logit link function was used to compare the number of eggs laid (a score of 0 equals one egg laid and a score of 1 equals two eggs laid) to the body mass of the lighter, and thus assumed to be female, bird (stats package in R v. 3.1.2; R Core Team 2014).

Results

I collected data from and monitored 18 African penguin nests on Robben Island over two years (8 nests in 2013 and 10 nests in 2014). 22 chicks in total were produced amongst all study nests (9 chicks in 2013 and 13 chicks in 2014).

The mass of the lightest bird in the pair significantly affected the number of chicks that fledged from the nest ($F_{(1,\ 14)} = 14.36$, $p = 0.002$; Figure 2.3). Birds with an exceptionally small mass of < 2.0 kg did not fledge any chicks, but when a bird weighed > 2.4 kg they always fledged two chicks. The mass of the heaviest bird in the pair, on the other hand, did not significantly affect the number of chicks that fledged ($F_{(1,\ 14)} = 1.44$, $p = 0.25$; Figure 2.4). When the mass of the two birds in a pair was averaged the result was once again significant ($F_{(1,\ 14)} = 5.16$, $p = 0.04$; Figure 2.5). There were no significant differences in the number of chicks fledged between the two years for all three mass variables (all $p > 0.05$, $n = 18$).

I also compared these same weights to the fledging period of each chick that fledged from the nest. In 2013, a fledging period of 58 days was recorded, and in 2014 two fledging periods of 56 days and 53 days were recorded. These fledging periods are quite short for this species, as chicks usually do not fledge until 75–80 days of age (Seddon and van Heezik 1993) and periods of this length are sometimes excluded as large chicks may wander from their nests and evade detection (Sherley *et al.* 2013). The data were therefore analysed with and without these outliers.

When the outliers of 53, 56, and 58 days were excluded from the data, fledging period was not significantly affected by the mass of the lightest bird ($F_{(1,\ 7)} = 1.80$, $p = 0.22$), the mass of the heaviest bird ($F_{(1,\ 7)} = 4.89$, $p = 0.06$), nor the mean mass of the two ($F_{(1,\ 7)} = 4.19$, $p = 0.08$). However, the mass of the heaviest bird is close to being significant and shows a trend for heavier adults to fledge chicks over a fewer days (Figure 2.6). There was a significant difference in fledging periods between the two years (all $p < 0.05$, $n = 11$). The mean fledging period was shorter in 2014 than it was in 2013 and the difference in means was significant (two sample t-test: $t_{(9)} = 3.41$, $p = 0.008$). When the outliers of 53, 56, and 58 days were included in the data there were no significant effects of body mass or year on fledging period (all $p > 0.05$, $n = 11$). This is likely because a fledging period of < 60 days is unusual (Seddon and van Heezik 1993).

The weight of the chicks at fledging was not significantly affected by the mass of the lightest bird ($F_{(1, 13)} = 0.04$, $p = 0.84$), the mass of the heaviest bird ($F_{(1, 13)} = 0.30$, $p = 0.59$), nor the mean mass of the two ($F_{(1, 13)} = 0.06$, $p = 0.81$). The proportion of eggs hatched from the number of eggs laid (hatching success) was not significant based on the mass of the lightest bird ($F_{(1, 14)} = 2.34$, $p = 0.15$), the mass of the heaviest bird ($F_{(1, 14)} = 0.26$, $p = 0.62$), nor the mean mass of the two ($F_{(1, 14)} = 1.29$, $p = 0.27$). The probability of a clutch with two eggs was not significantly affected by the mass of the lighter, presumably female, bird (coefficient estimate = 4.19, $z_{16} = 1.49$, $p = 0.14$). Although not significant, there is a trend for heavier females being more likely to lay two eggs (Figure 2.7).

Discussion

In this study I related body mass at the onset of breeding to the breeding success of African penguins on Robben Island. I expected that the body mass of either bird in a pair could have an influence on breeding success.

The adult with the larger mass had no effect on the number of chicks that fledged. The body mass of the lighter bird, however, did have an effect, with an increase in the number of chicks that fledged as body mass increased. When the lighter bird in a pair weighed less than 2.0 kg, no chicks were fledged, but when that bird weighed more than 2.4 kg two chicks always fledged. As I predicted, body mass affected the number of fledged chicks, but only when the body mass of the lighter bird was taken into account.

If one individual has a low body mass it may be unable to provide an equal amount of effort. African penguins share parenting duties throughout incubation (Randall 1983) and chick-rearing. The partner of a bird in poorer condition must be in good enough condition to be able to compensate and continue to meet the chicks' needs. This would be especially difficult for penguins because of a long breeding season (Randall 1983). Paredes *et al.* (2005) speculated that the willingness of one member of a pair to compensate for poor performance of the other in long-lived species is based on the costs of parental effort and the likelihood of breeding failure.

A nest at the incubation or young chick stage would be most at risk of failure if one parent is in poor condition because that parent may spend a longer time foraging to build up its own reserves (Clarke 2001), while the other partner must stay at the nest until the foraging bird returns (Lei *et al.* 2014, Numata *et al.* 2000). The partner at the nest may leave the nest to avoid starvation if not relieved in time, which would leave the nest contents vulnerable to breeding failure (Davis 1982, Numata *et al.* 2000). In this study, three out of four of the nests that produced no chicks to fledging were abandoned at the incubation stage. At one of the nests where no chicks fledged, two chicks were found dead just over 30 days after hatching. It was also the nest that had the bird with the smallest mass in the study.

Harding *et al.* (2009) and Paredes *et al.* (2005) both studied the implications when a partner in a pair is handicapped. Harding *et al*. (2009) tested this by manipulating little auk *Alle alle* pairs by feather clipping one of the birds. This resulted in a decrease in body mass and parenting effort of the bird that was feather clipped. Partners of handicapped birds also lost body mass suggesting that they were trying to compensate for the lack of effort by their partner. These manipulated nests produced chicks with a lower mass at time of hatching, indicating that there may be a point where the partner must consider its own condition over provisioning the chick. Paredes *et al.* (2005) looked into the effects of thick-billed murres *Uria lomvia* equipped with time-depth recorders. Nests that had one of the partners handicapped resulted in reduced feeding effort by that partner. The partner that was not handicapped increased feeding rates to equal the amount delivered before the other partner was handicapped. In this case, when there was adequate food availability, birds were able to compensate for their partner by increasing their individual effort.

I predicted the fledging period of chicks to be shorter for pairs with a higher body mass, as it was expected that they would be more efficient at provisioning their chicks (Saraux *et al.* 2011). However, neither the mass of either adult nor the average mass had any significant effect on the fledging period; although, as shown in figure 2.6, there is a trend for the fledging period to be shorter when the heavier partner has a larger body mass at the onset of breeding. It is possible that this trend in shorter fledging periods could either be confirmed or eliminated if the data set were larger. Fledging periods less than 60 days are considered unusually short (Sherley *et al.* 2013), but when these were excluded from the data there was still no significant effect except that the mass of the heavier adult once again showed a trend of having shorter fledging periods as mass increased. There was a difference in fledging period between years. Recorded fledging periods ranged between 74–85 days in 2013, and 65–80 days in 2014. Fledging periods were reported to be longer when food availability was low prior to breeding (Sherley *et al.* 2013), so differences in food availability among years could affect the length of the fledging period.

The probability of the lighter, female bird laying a clutch of two eggs was not affected by body mass. It was thought that more energy, that a lighter bird may not have, would be needed to lay a larger clutch. This result, however, is not entirely unexpected as the mean clutch size for African penguins on Robben Island is 1.86 and shows little interannual variability (Crawford *et al.* 1999). Hatching success was also not determined by the body mass of either adult. It is more likely that adults with a lower body mass would struggle more during chick-rearing when they must spend extra energy provisioning their chicks, rather than during incubation. Parents that have a greater ability to provision their chicks and provide equal effort are more likely to fledge heavier chicks (Saraux *et al.* 2011).In this study, heavier adults did not produce heavier chicks at fledging, contrary to my prediction.

This study provides evidence that body mass carried over from the onset of breeding can have an effect on breeding success in African penguins. Salton *et al.* (2015) reported a carry-over effect in little penguins, finding that birds with a greater body mass during the non-breeding season were more likely to be successful and to start breeding early. There have also been other studies describing the benefits of built-up reserves carrying over into the subsequent breeding season. Red knots *Calidris canutus islandica* that had body stores carried over from migration survived extreme weather during the breeding season that otherwise caused poor breeding success and mortality (Morrison *et al.* 2007). Robb *et al.* (2008) found that supplementary feeding of blue tits *Cyanistes caeruleus* before the start of breeding improved breeding productivity.

There was no variation between years, except with fledging period. It is still possible that effects may be more apparent in years of poor local food availability. If there are adequate food resources throughout breeding, a bird in poor condition may still be able to successfully raise its chicks, whereas if local resources are poor than a bird in already poor condition would be likely to fail. It is also possible that even though a bird is in good condition, it would still not be enough to ensure survival if local feeding conditions during breeding are poor (Sherley *et al.* 2013). Harrison *et al.* (2013) related reproductive success of light-bellied Brent geese *Branta bernicla hrota* with carry-over effects from the season before breeding, but only under certain environmental conditions. If conditions were poor during the breeding season then there was no advantage of having a higher body mass. More years of study may make it possible to determine if effects vary between years, and comparing the results to data on food availability may determine if effects are greater during years of poor food availability prior to breeding.

Nevertheless, the presence of a carry-over effect of body mass improving breeding success highlights the importance of an adequate availability of food resources during the non-breeding season for African penguins. Capital breeders rely on building up reserves before the start of breeding because they breed in an unpredictable environment whereas income breeders rely on gradually accumulating their reserves from local food resources (Jönsson 1997). It is likely that African penguins are both capital and income breeders. They rely on local food availability during the breeding season, but since they are not constrained to their breeding grounds when they are not breeding, they may be able to use more distant prey to gain body mass prior to breeding (Durant *et al.* 2010). Ideally, sufficient resources must be available throughout both the breeding season and the non-breeding season (Sherley *et al.* 2013).

Body mass alone as a measure of condition can be limiting, as it does not account for structural size. A heavier bird may not necessarily be in better condition than a lighter bird (Labocha and Hayes 2012). Therefore, an adult body condition index for this species would help to account for differences in body size (Golet *et al.* 1998), allowing for a better interpretation of the data, similar to the chick condition index used for African penguins (Lubbe *et al.* 2014). This study was designed to reduce disturbance at the nest by not handling the adults, and therefore no structural measurements were taken as birds are generally handled to obtain mass and body measurements. If it is possible to estimate a structural size through the use of imagery by using objects of known size, then it would eliminate the need to handle the birds, while still producing a body condition index.

Finally, this study tested new techniques that resulted in periods of trial and error and because of this relatively small sample sizes were produced, and only a small number of replicates were obtained. When such a small data set is involved it is difficult to make any substantial conclusions. These findings, however, could contribute to a longer-term study if more data is collected and the techniques described in this study have the potential to be improved and expanded on.

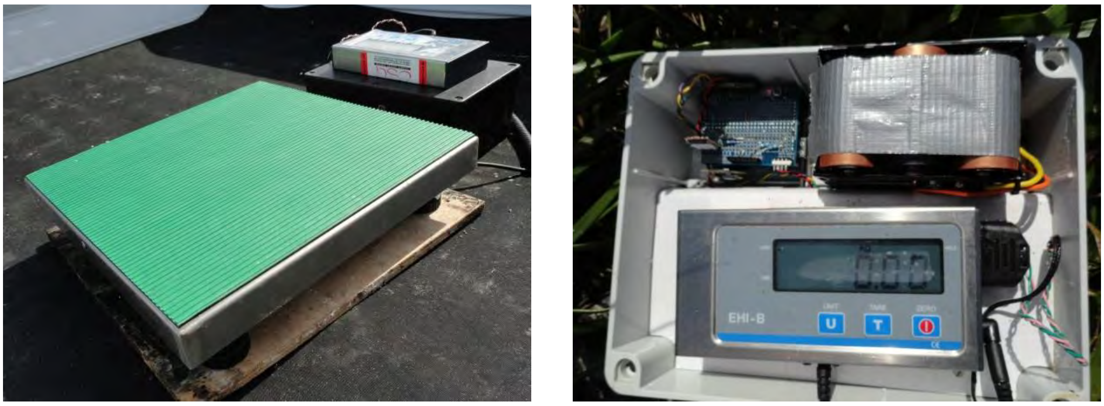

Figure 2.1 PS-105 Parcel Scale (30 cm x 30 cm) with weight reader, data logger, and six D-cell batteries.

Figure 2.2 The scale inside a dry bag (upper left) set up in front of an African penguin *Spheniscus demersus* nest on Robben Island with a camera trap opposite to capture images (lower right, on the tree stump).

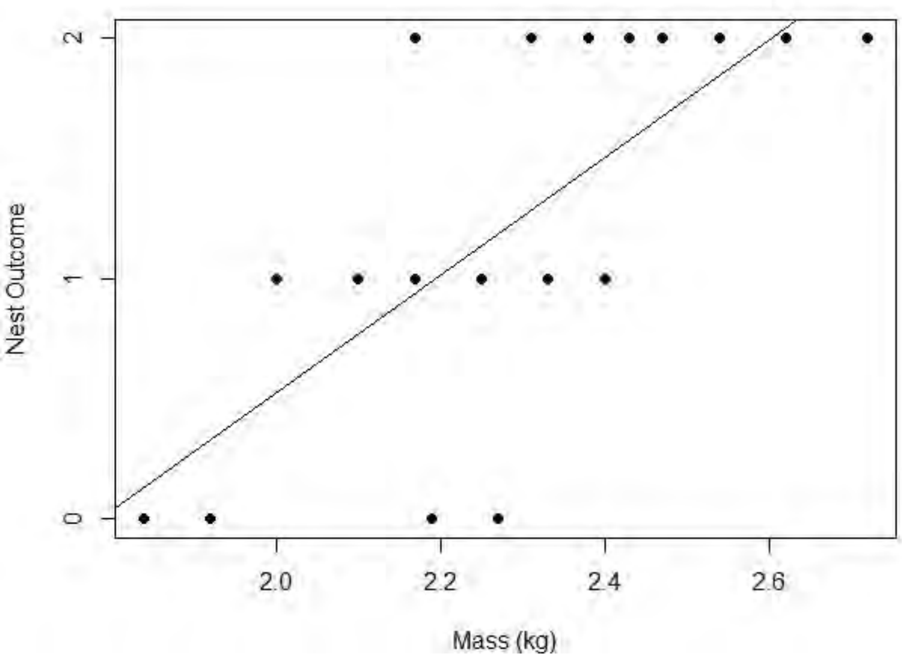

Figure 2.3 The relationship between the Nest Outcome (no. of chicks fledged from 0 to 2) of (n=18) African penguin *Spheniscus demersus* nests monitored in 2013 and 2014 and the body mass (kg) of the lightest adult in the breeding pair. The solid line represents the linear regression fit.

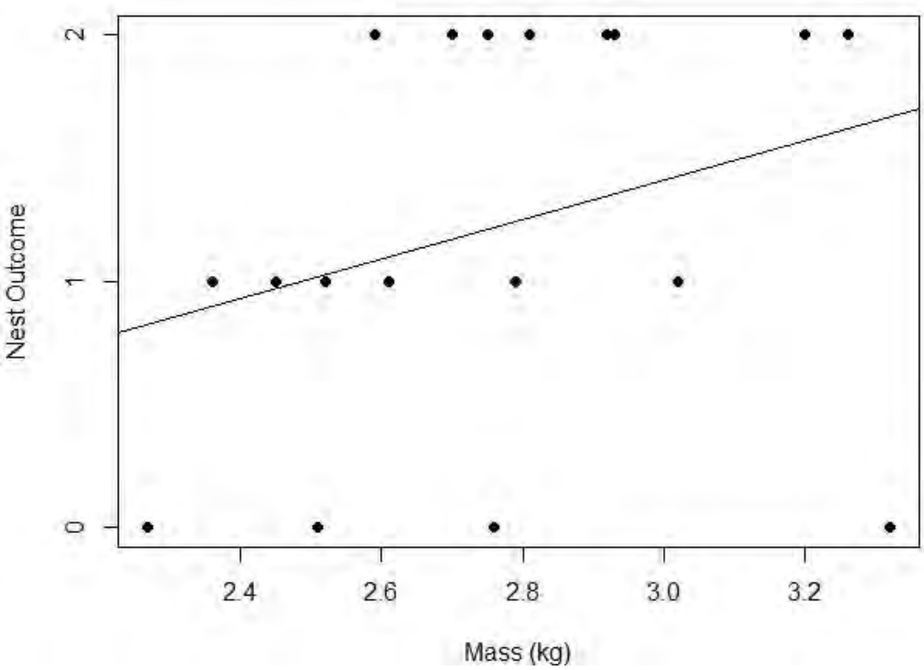

Figure 2.4 The relationship between the Nest Outcome (no. of chicks fledged from 0 to 2) of (n = 18) African penguin *Spheniscus demersus* nests monitored in 2013 and 2014 and the body mass (kg) of the heaviest adult in the breeding pair. The solid line represents the linear regression fit.

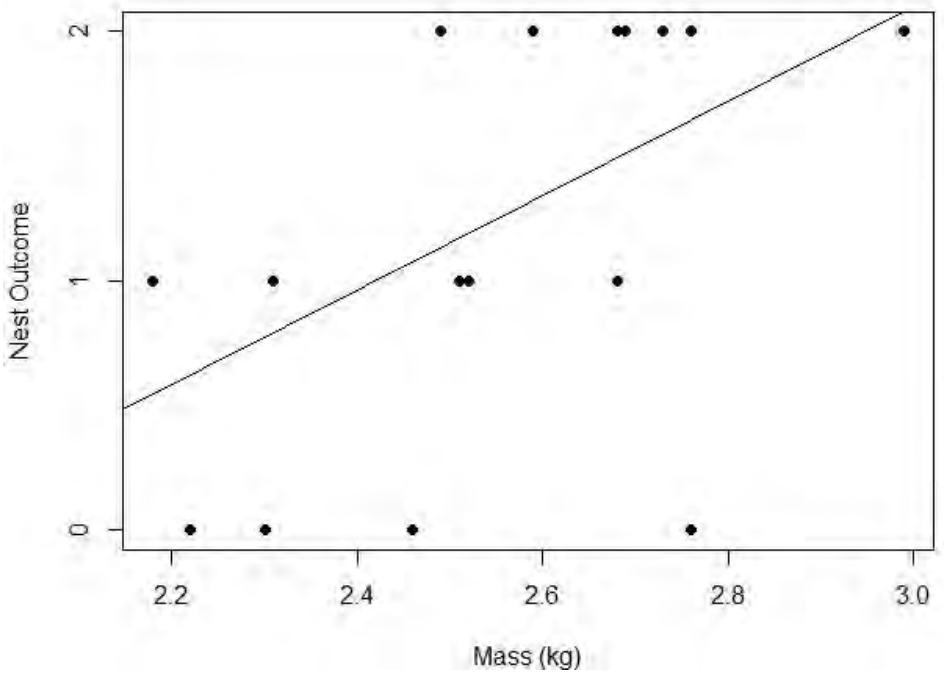

Figure 2.5 The relationship between the Nest Outcome (no. of chicks fledged from 0 to 2) of (n = 18) African penguin *Spheniscus demersus* nests monitored in 2013 and 2014 and the body mass (kg) of the combined mean mass of the breeding pair. The solid line represents the linear regression fit.

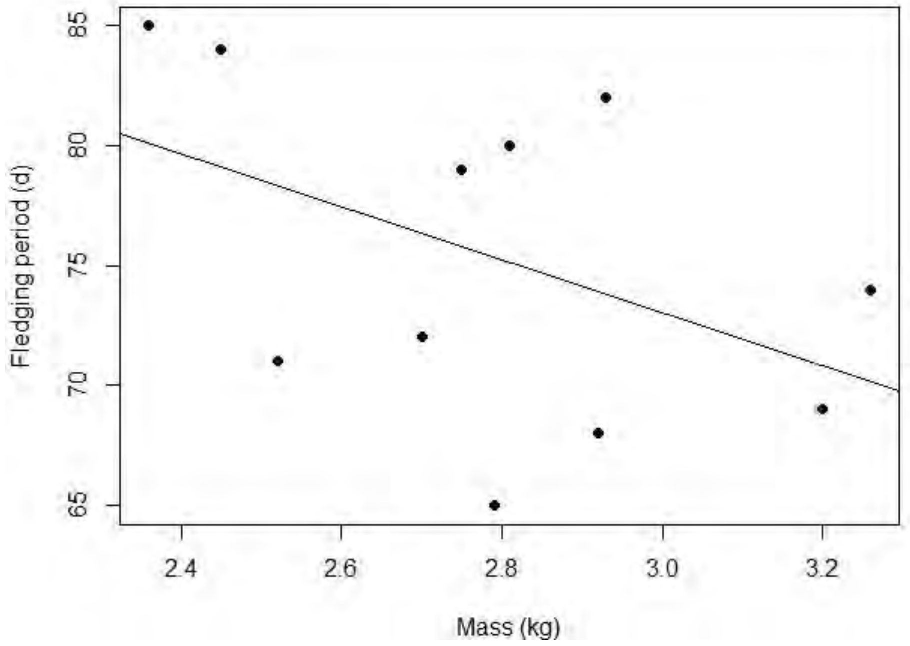

Figure 2.6 The estimates for the mean fledging period (days) of African penguin *Spheniscus demersus* chicks from (n = 11) successfully monitored nests in 2013 in relation the body mass (kg) of the heaviest adult in the breeding pair. Fledging periods of < 60 days are excluded from these data. The solid line represents the linear regression fit.

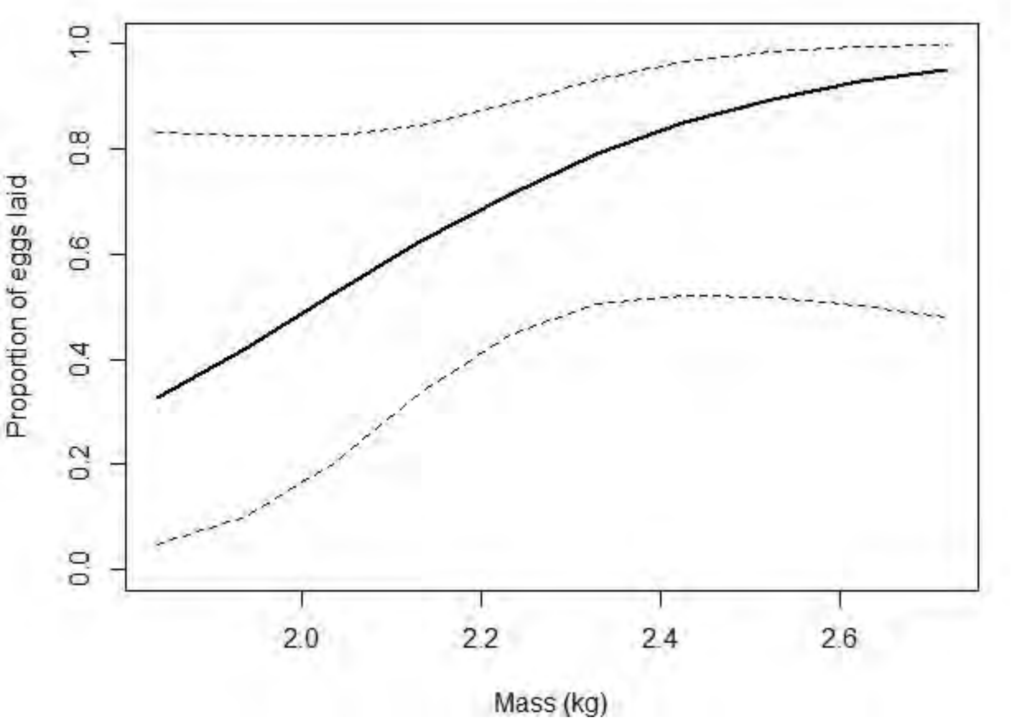

Figure 2.7 A generalized linear model (GLM) with a binomial error distribution and a logit link function was used to compare the probability of a clutch with two eggs (0 = one egg laid, 1 = two eggs laid) to the body mass (kg) of the lightest, presumably female, adult in the breeding pair from (n = 18) monitored African penguin *Spheniscus demersus* nests in 2013 and 2014. The dashed lines represent 95% confidence intervals.

Chapter 3

The influence of climatic conditions on the suitability of African penguin nests on Robben Island

Abstract

Extreme weather events can be detrimental to seabird breeding success and survival. African penguins rely on sheltered nest sites during breeding to protect them from rain and high temperatures. African penguins on Robben Island nest mostly under vegetation, but they also nest in disused buildings, wooden nest boxes, artificial fibreglass burrows, natural burrows, and on the surface. This study compared nest failure during incubation and chick rearing with rainfall and maximum temperature for the types of nests used by breeding African penguins on Robben Island. Rain caused increased failure for both eggs and chicks regardless of nest type, whereas temperature caused an increase in incubation failure based on nest type. This study also recorded operative temperatures within artificial burrows, nest boxes, vegetation nests, and on the surface. Nests under vegetation recorded the lowest temperatures, while surface nests recorded the highest temperatures. Temperatures recorded inside artificial nests (nest boxes and artificial burrows) were lower than temperatures recorded on the surface, demonstrating that they are able to provide some protection from high ambient temperatures, and solar radiation. Nest failure rates of artificial nests were no higher than natural nests, and so they can be considered as a suitable nesting alternative. Artificial nests, however, did record higher temperatures than nests under vegetation, which suggests that more work on design and placement of artificial nests is needed to create an optimal alternative nesting habitat.

Introduction

Climate change is predicted to result in an increase of extreme weather events, such as heavy rainfall, storms, severe temperatures, and drought (Catry *et al.* 2011). Global mean surface temperatures are projected to rise, resulting in frequently higher temperatures. It is believed that the frequency and duration of heat waves and larger rainfall events will also become more common (IPCC 2014). In the western part of South Africa, there has been a noticeable trend of higher than average maximum temperatures (Kruger and Sekele 2013). New *et al.* (2006) also reported that southern Africa and other regions are showing signs of climate change based on temperature extremes, and an increase in the number of hot days and nights.

Climate change events, such as higher temperatures, can have a significant impact on seabird phenology, demography, distribution, and behaviour (Crick 2004, Parmesan 2006). Rising temperatures can have both direct (e.g. thermoregulation) and indirect (e.g. food availability) effects on seabirds (Oswald and Arnold 2012).

Increased temperatures result in greater thermoregulatory demands. This can lead to thermal constraint in breeding seabirds as more of the birds' energy would go towards thermoregulation, at the expense of reproduction and growth (Oswald and Arnold 2012). This increased expense in energy could lead to a greater risk of death for adults and chicks. Oswald *et al.* (2011) found that the distribution of species was negatively affected by direct constraints from climate.

Indirect effects of climate can include changes in quality and availability of food (Durant *et al.* 2003) and habitat (Batianoff *et al.* 2010). For example, the effect of increasing temperatures caused by climate change is demonstrated by the extensive warming and melting of sea ice. The reproduction of Brunnich's guillemots *Uria lomvia* in the southern part of the species' range has been negatively affected by decreased ice cover due to warming (Gaston *et al.* 2005) and Trathan *et al.* (2011) documented the loss of an emperor penguin *Aptenodytes forsteri* colony over a period of rising mean local air temperatures and a decrease in seasonal sea ice duration.

Seabirds are endothermic; they have a range of environmental temperatures (thermal neutral zone) at which the amount of energy used in thermoregulation is low. If temperatures reach below or above this range, a greater amount of energy must be used to maintain thermal homeostasis (Oswald and Arnold 2012). Seabirds keep their body temperature regulated closer to the upper thermal limit, thus they can maintain their body temperature during colder temperatures; however, even a slight increase in environmental temperature can lead to heat stress and hyperthermia (Lustick 1984). The birds' body temperatures are often determined by ambient air temperatures but can also be affected by the birds' own thermal properties and external climatic variables. For example, heat gain can also come from metabolic heat production and solar radiation (Oswald and Arnold 2012).

During the early stages of breeding, seabirds must stay at the nest, either incubating eggs or brooding small chicks, and have behavioural and physiological adaptations for thermoregulation when coping with heat stress (Randall 1983). Some of these methods of heat loss include convection, conduction, evaporation, and postural adjustments (Oswald and

Arnold 2012). Convective heat loss is increased by maximizing the exposure of a bird's surface to air flow, and by increasing blood flow to the legs and feet (Dawson 1982). Conductive heat loss is mainly through the contact of the legs and feet with the ground, but when ground surface temperatures are high, exposing the body to water will greatly increase heat loss (Oswald and Arnold 2012). Evaporative heat loss is the most effective method. This is accomplished by both cutaneous evaporation and respiratory evaporation by panting and gular fluttering (Wolf and Walsberg 1996). This method, however, can lead to osmotic stress and may result in a breeding bird temporarily abandoning the nest to drink (Hand *et al.* 1981, Randall 1983). A bird will adjust its posture and orientation to minimize the exposure of darker plumage to the sun (Randall 1983), as dark plumage can increase the thermal load from solar radiation (Oswald and Arnold 2012).

If high temperatures persist, the bird at the nest may ultimately be forced to temporarily abandon it to cool down and rehydrate (Randall 1983), leaving the nest contents vulnerable, and most likely leading to breeding failure. Frost *et al.* (1976a) and Randall (1983) observed African penguins leaving the nest to go to the sea after a prolonged period of panting; nest abandonment seemed to be the last resort to cope with heat stress. Chicks can also become heat stressed during periods of high temperatures if they are not properly shaded (Randall 1983). Thermoregulatory behaviours increase water loss in both adult and chick seabirds. Adults can obtain water from drinking while foraging, but chicks are likely to succumb to dehydration as they rely solely on ingested food for their water intake (Campbell 2014).

Penguins live a mostly aquatic lifestyle, but must come to land to breed and moult. They have evolved to feed in a marine environment with a thermal conductivity approximately 24 times greater than that of air (Lustick 1984). This means that penguins are well insulated against heat loss in cold water, but are susceptible to hyperthermia on land because of the decrease in thermal conductance (Frost *et al.* 1976a). This is especially a problem for African penguins as they breed in a Mediterranean climate, and can be subjected to hot temperatures while on land.

Storms and rainfall also have the potential to cause breeding failure in seabirds (Boersma and Rebstock 2014, Sherley *et al.* 2012a). A period of high winds, heavy rainfall, and low temperatures caused the death of a large number of Arctic tern *Sterna paradisaea* and common tern *Sterna hirundo* chicks (Robinson et al. 2002). Heavy rain can cause African penguin nests to flood and burrows to collapse (Frost *et al.* 1976a) leading to inundated eggs, drowned chicks and deaths due to hypothermia (de Villiers 2002). Similar mortality has also been noted in the closely related Magellanic penguin (Boersma and Rebstock 2014). Adults may desert their eggs when there is heavy flooding and young chicks are not yet thermally independent, making them more susceptible to death by exposure if not protected by the adult (Wilson and Wilson 1989). Even larger chicks, if they do not yet have their waterproof plumage, may not be able to maintain their body temperature if they get wet (Boersma and Rebstock 2014).

Adequate nesting habitat for seabirds is vital to ensure survival and protection from extreme environmental conditions. For example, the nesting habitat of European storm petrels *Hydrobates pelagicus* has deteriorated due to erosion, causing burrows to collapse and competition for breeding space with other seabirds. This has resulted in a large decrease in breeding numbers over time (Cadiou *et al.* 2009). African penguins historically nested in burrows or on the surface (Frost *et al.* 1976a). Burrows provide the cover necessary to protect from extreme weather events and predation, and they maintain a more constant microclimate (Frost *et al.* 1976a). To create these burrows, African penguins would dig into the accumulated guano. Guano, however, was exploited for use as a fertilizer which resulted in the removal of guano from all island colonies in South Africa (Wilson and Wilson 1989). This meant that penguins often had to occupy suboptimal breeding habitats, such as nesting on the surface with no cover to provide protection. These nests are completely exposed to high ambient temperatures, solar radiation (Randall 1983), and flooding. If an adult leaves the nest, the contents are immediately vulnerable to predation (Seddon and van Heezik 1991). Bank cormorants on Robben Island breed in nests that are completely exposed, and they have experienced nest failures during storm events and periods of high air temperatures (Sherley *et al.* 2012a).

Artificial nests have been installed in some breeding colonies to improve the survival of seabirds (e.g. Libois et al. 2012), and various types of artificial nests have been developed and put in place for African penguins to provide nesting habitat that helps with protection from environmental variability and predation (Kemper *et al.* 2007a, Pichegru 2013, Sherley *et al.* 2012b). However, artificial nests that inadequately replicate natural nesting conditions have the capacity to act as ecological traps (Sutherland *et al.* 2014) and some designs of artificial nests for African penguins may produce microclimates that are not conducive to breeding (Lei *et al.* 2014).

In this chapter I aim to determine if egg and chick mortality vary as a function of nest type, relate egg and chick mortality to selected environmental conditions and to examine whether any responses differ according to nest type, determine temperature variations within nest types, determine effect of orientation on nest box temperature, and show that mean maximum temperatures and rainfall have increased on Robben Island over a certain number of years.

Rainfall and high temperatures can cause the failure of penguin nests (Boersma and Rebstock 2014, Sherley *et al.* 2012a), but survival probabilities can vary depending on the type of nest, with artifical nests providing more protection than nests that are more exposed (Sherley *et al.* 2012b, Wilson and Wilson 1989). I expected artificial nests to have the lowest incidence of nest failure, because of this extra protection, while I expected open nests would have the greatest degree of failure (Sherley *et al.* 2012b, Wilson and Wilson 1989).

Frost *et al.* (1976a) compared operative temperatures of surface nests to temperatures within burrows and found that temperatures in the burrows were more constant, and cooler throughout the day, than ambient temperatures and temperatures on the surface. Randall (1983) made similar comparisons using an artificial concrete nest and obtained similar results when comparing to surface temperatures. Just like the burrow nests, these artificial nests recorded cooler temperatures than nests on the surface. In contrast, Lei *et al.* (2014) found that artificial nests (cement and fibreglass) recorded higher temperatures for longer durations of time than natural burrow nests. I expected there to be differences in temperatures between nest types and that they would differ from ambient and surface temperatures.

The placement of artificial nests may be an important consideration as it could have an effect on the conditions within the nest. Butler *et al.* (2009) recorded lower average temperatures in nest boxes facing west, compared to nest boxes facing east and south. I predicted that the orientation of nest boxes would result in variations in recorded temperatures within each nest box.

Climate studies for South Africa have shown increasing trends in maximum temperatures (Kruger and Sekele 2013) and rainfall (Kruger 2006, New *et al.* 2006). Similar trends with temperature can be seen in the long-term data for Robben Island so it is probable that these changes will continue into the future.

Materials and methods

Nest failure and weather data

I used data collected from 2001–2013 as part of a long-term monitoring project of the African penguins on Robben Island. A number of nests (between 70 and 274) were selected and monitored each year using consistent methods to determine breeding success (e.g. Sherley *et al.* 2012b).

The monitoring period usually lasted from March until August; however it varied in certain years with checks starting in February or continuing until November (Sherley *et al.* 2012b). All nests were monitored at the same rate, usually within two days, so disturbance was equal amongst nest types. The intervals between nest checks were usually six days but could vary; they were sometimes as short as four days or as long as 28 days when logistics precluded access to the colony (Sherley *et al.* 2012b).

The total number of active nests and the total number of failed nests per year were extracted from the data. A nest was considered active if it had eggs or chicks, and a nest was considered to have failed if it was abandoned, eggs failed to hatch, or chicks died. Active and failed nests were separated into whether they were at the incubation stage or the chick rearing stage, so that nest failure could be determined separately for eggs and chicks. Each year was then split into monitoring intervals to determine the number of failures after each new check. For example, if a nest was reported as incubating eggs during a check and then reported as abandoned at the next check, the nest was assumed to have failed at some time during the intervening period.

I further split the data into nest types to be able to determine any variation in breeding failure based on nest type. This study incorporated six of the types of nests used by breeding penguins on Robben Island. These nests were classified as vegetation, open, natural burrow, building, nest box, and artificial burrow (Sherley *et al.* 2012b). Vegetation nests are the most commonly used by breeding pairs and are defined as shallow scrapes in the ground with vegetation, predominately rooikrans, providing some cover (Figure 3.1). The amount of cover varies to some degree for each nest depending on the type of vegetation and how much is present. Open nests are shallow scrapes completely exposed with no cover provided by any substrate. Natural burrows are created when a breeding penguin burrows into the ground to make a nest, creating a burrow that provides complete cover. Building nests can be found in any disused building or other man-made object that provides complete cover (Figure 3.2). The artificial nests on Robben Island are comprised of two types; nest boxes and artificial burrows. The nest boxes were first installed in 2001, and are free-standing and made of plywood with an A-frame design (Figure 3.3). Nest box placement and orientation varied throughout the colony, with some placed in the open and others partially or completely under vegetation. The artificial burrows were put in place in 2007 and are made of fibreglass and resin mesh and built to resemble a natural penguin burrow. They were partially buried and covered with soil and rocks, but the degree of cover has varied over time because of the effects of rain and wind causing erosion (Figure 3.4, Sherley *et al.* 2012b).

I then split the data into two time periods; 2001–2013 and 2007–2013. This is because data were not available for artificial burrows before 2007 and a separate analysis was conducted to compare artificial burrows to nest boxes and vegetation.

Weather data obtained from the South African Weather Service station on Robben Island were used to compare total rainfall and daily maximum temperature to the breeding failure rate of various nest types.

Long-term temperature data for maximum temperature (1975–2012) was obtained from the South African Weather Service station situated at Cape Town International Airport, and used as a proxy for Robben Island as data from the island do not go back as far. Total rainfall (1950–2012) was obtained from the Robben Island weather station.

Temperature data and comparisons between nest types

It is likely that conditions inside a nest will vary from those outside, which may make it difficult to determine differences between nest types based on outside weather variables. For example, rain may be more likely to affect all nests similarly, whereas temperature experience within a nest may vary more between nest types. To test these ideas, I recorded operative temperatures within nests to see if there were differences in the temperatures birds would experience in difference types of nest. Operative temperatures (T_e) were recorded within wooden nest boxes, artificial fibreglass burrows, under vegetation, and on the surface to get an idea of the conditions inside these nests, as temperatures inside would likely vary from outside air temperatures. T_e accounts for the environmental temperature experienced by a specific animal (Bakken *et al.* 1985). Ambient temperature (T_a) was also recorded. Temperatures were recorded following the similar methods of Campbell (2014) and Meyer

(2014). iButtons (Thermochron iButton model DS1922L-F5#, Maxim/Dallas Semiconductor Corp.) recorded temperatures and were programmed to take readings every 10 minutes, with a temperature resolution of 0.0625°C and a range of –40°C to 85°C. ColdChain Thermodynamics software was used to program the iButtons and to download the data.

To measure T_a, two iButtons were suspended using wire inside a portable Stevenson screen (15 cm high, diameter 13 cm), which was in turn secured to a metal rod to aid placement in the field (Figure 3.5). To measure T_e, models were built from two copper alloy half-spheres (0.9 mm thick, diameter 11.5 cm when assembled) with a hole drilled through the middle of each. These were attached using TESA® tape and a metal support rod was inserted through the holes of the bottom and top halves and these were bolted together. The spheres were painted to match the reflectance and absorptance of the animal (Bakken 1985, Randall 1983). The bottom half-sphere was spray-painted matte white and the top half-sphere was spray-painted matte black, to resemble the black dorsal surface and white ventral surface of a penguin (Figure 3.5, Randall 1983). Wire secured to the metal rod was used to suspend two iButtons within the sphere, ensuring they did not touch each other or the sides of the sphere.

In many cases, models are built using taxidermic mounts, but these can be difficult to obtain, difficult to construct, costly, and less durable in the field (Bakken 1992). Hollow, painted copper spheres were used in this study because they have been shown to be a suitable alternative model for measuring T_e (Bakken *et al.* 1985, Walsberg and Weathers 1986).

A nest box was placed beside a previously installed artificial burrow, with the entrances facing in the same direction, with no extra cover from vegetation (Figure 3.3). A painted copper sphere was placed in each nest approximately 10 cm from the ground. A sphere and a Stevenson's screen were placed in the open beside the nests, approximately 10–20 cm from the ground (Figure 3.5). The sphere was used to estimate the T_e experienced by birds nesting in the open and the Stevenson's screen recorded T_a. This set up was replicated at various locations of previously installed artificial burrows. Vegetation nests were also compared alongside nest boxes and artificial burrows, and to do this a sphere was placed in the ground under vegetation as close to the other nests as possible. Vegetation covers most of the colony and it was always possible to access an area of vegetation very close by. The amount of cover does vary in vegetation nests, but I tried select areas with similar cover for each replicate.

Orientation effect

The effect of orientation on temperature obtained in nest boxes was studied by placing four wooden nest boxes together in the field, with each one facing in a North, East, South, or West orientation (Figure 3.4). Orientation was determined by using a handheld GPS unit with a built-in GPS compass and walking in a straight line away from a nest box until North was determined. The orientation of the nest box was adjusted accordingly so that the entrance was facing north. This process was repeated with the other three nest boxes to determine East, South, and West. Each nest box contained a painted copper sphere, while a Stevenson's screen was placed outside to record ambient temperature.

Data Analysis

Generalized linear mixed-effects models (GLMM) with a binomial error distribution and a logit link function were used to determine which weather factors influenced nest failure, using the lme4 package in R v. 3.1.2 (R Core Team 2014). For both eggs and chicks, the response variable was the proportion of the nests active at each nest visit that failed in the following nest visit interval (the proportion of failed nests) for each nest type. Nest type, rain and maximum temperature were used as fixed effects, and the monitoring interval was used as the random effect. For all models, vegetation was set as the intercept for nest type because it was the most common nest type used by breeding pairs (Sherley *et al.* 2012b). For each time period and breeding stage, three candidate models were compared using the MuMIn package in R v. 3.1.2 (R Core Team 2014), and Akaike's information criterion adjusted for small samples sizes (AICc; Table 3.1). The best fitting model was selected based on a ΔAICc > 2 to the next best model and Akaike's weights (Burnham and Anderson 2002). To test for differences between nest types a generalized linear hypothesis test was used to conduct multiple pairwise comparisons of the model to test the significance of the means using Tukey contrasts (multcomp package in R v. 3.1.2; R Core Team 2014).

Linear mixed-effects models were used to compare maximum temperature and the range between minimum and maximum temperature (temperature amplitude) between nest types, using the nlme package in R v. 3.1.2 (R Core Team 2014). These temperature parameters were used as the dependant variables, and nest type and Julian days as the fixed effect, with nest ID as the random effect. A generalized linear hypothesis test was used to conduct multiple pairwise comparisons of the model to test the significance of the means using Tukey contrasts (multcomp package in R v. 3.1.2; R Core Team 2014).

Generalized linear mixed-effects models were used to compare proportion of hours per day above 30°C and 25°C between nest types, using the lme4 package in R v. 3.1.2 (R Core Team 2014). The temperature proportion was used as the dependant variable, and nest type and sampling intervals were used as the fixed effects, with nest ID as the random effect. Sampling interval instead of Julian day was used as the fixed effect in this model because the model did not converge when Julian day was used, likely due to a very strong time of year effect.

The proportion of time the temperature exceeded 30°C was used following Lei *et al.* (2014), who chose this temperature based on the heat stress point of the closely related Humboldt penguin *Spheniscus humboldti* (Drent and Stonehouse 1971). Frost *et al.* (1976a) conducted a laboratory study of African penguins and found body temperatures starting to increase once ambient temperatures reached 33°C, but in the field they started to increase when temperatures started to exceed 27°C. Penguins started panting once ambient temperatures started to exceed 28°C, and in the field these behaviours were already apparent at temperatures exceeding 24°C so temperatures above 25°C were also analysed.

A generalized linear mixed-effects model with a binomial error distribution and a logit link function (lme4 package in R v. 3.1.2; R Core Team 2014) was used to compare orientations of wooden nest boxes. Temperature proportion was used as the dependant variable, and orientation was used as the fixed effect, with Julian days as the random effect.

A simple linear model (stats package in R v. 3.1.2 R Core Team 2014) was used for long-term weather data to analyse total monthly rainfall and the proportion of days per year where temperatures exceeded 30°C, for the months of February, March, and April as this is when most clutches are laid on Robben Island (Crawford *et al.* 1995).

Results

Nest failure and weather data

Nest failure from 2001–2013 varied significantly between nest types at both the incubation stage ($\chi^2 = 10.76$, df = 4, p = 0.03; Figure 3.7) and the chick-rearing stage ($\chi^2 = 21.93$, df = 4, p = 0.02; Figure 3.8). Nest failure from 2007–2013 still varied between nest types at the chick-rearing stage ($\chi^2 = 11.28$, df = 2, p = 0.004; Figure 3.8), but it was no longer significant during incubation ($\chi^2 = 0.045$, df = 2, p = 0.98; Figure 3.7). During incubation nest boxes had the lowest failure rate and differed significantly from vegetation nests (coefficient estimate =

2.52, $z_{769} = 2.93$, $p = 0.03$) and open nests (coefficient estimate = 3.86, $z_{769} = 2.71$, $p = 0.048$). During chick-rearing, nest boxes also had the lowest failure rate and differed significantly from vegetation nests (coefficient estimate = -0.57, $z_{939} = -3.03$, $p = 0.02$), natural burrows (coefficient estimate = -0.91, $z_{939} = -2.91$, $p = 0.03$), and open nests (coefficient estimate = -1.03, $z_{939} = -3.72$, $p = 0.002$). Building nests also had a significantly lower failure rate than open nests (coefficient estimate = 0.99, $z_{939} = 3.30$, $p = 0.008$). Artificial burrows had a significantly lower failure rate than vegetation nests (coefficient estimate = -1.60, $z_{508} = -2.73$, $p = 0.01$).

The model with the best fit for the incubation data had nest type, rain, and maximum temperature as the explanatory variables, and included an interaction term between the nest type and maximum temperature. The preferred model was the same for both the data from 2001–2013 and the data that included artificial burrows from 2007–2013. (Table 3.1, Model 2). Even though the ΔAICc of Model 1 was within 2 units, Model 2 was still selected as the preferred model for 2007–2013 because it was the simpler model, while still containing the same parameters (Arnold 2010) and the AICc weight also supported the selection of Model 2. The model with the best fit for the chick-rearing data had nest type, rain, and maximum temperature as the explanatory variables, with no significant interaction terms. The preferred model was again the same for both the data from 2001–2013 and the data from 2007–2013 (Table 3.1, Model 3).

Nest failures during incubation increased with increasing rainfall for all nests (2001–2013: coefficient estimate = 0.01, $z_{769} = 3.29$, $p < 0.001$; Figure 3.9). Rainfall did not have a significant effect when artificial burrows were included in the data from 2007–2013 (coefficient estimate = 0.01, $z_{412} = 1.92$, $p = 0.05$). Increases in temperature did not significantly affect nest failure for all nests (2001–2013: coefficient estimate = 0.04, $z_{769} = 1.92$, $p = 0.05$, 2007–2013: coefficient estimate = 0.03, $z_{508} = 1.28$, $p = 0.20$), but temperature did show a significant difference between nest types. Figure 3.10 shows the model for the 2001–2013 time period ($\chi^2 = 14.94$, df = 4, $p = 0.005$) and figure 3.11 shows the model for the 2007–2013 time period ($\chi^2 = 8.99$, df = 2, $p = 0.01$). All nests types (vegetation, natural burrow, open, building, artificial burrow) displayed increasing trends in nest failure with temperature, except for nest boxes, which displayed a decrease in nest failure as temperatures increased. Nest boxes were the only nest type to differ significantly from vegetation nests (2001–2013: coefficient estimate = -0.10, $z_{769} = -2.96$, $p = 0.003$; 2007–2013: coefficient estimate = -0.12, $z = -2.97$, $p = 0.003$).

Nest failures for all nests during chick-rearing increased with increasing temperatures; figure 3.12 shows the effect for the time period 2001 – 2013 (coefficient estimate = 0.11, z_{939} = 5.99, $p < 0.001$) and figure 3.13 for the time period 2007- 2013 (coefficient estimate = 0.09, z_{508} = 4.24, $p < 0.001$). The proportion of nest failures was lower from 2007–2013 than it was from 2001–2013 (Figure 3.12, 3.13). Similarly to incubation, rainfall no longer had a significant effect on nest failure during chick-rearing when artificial burrows were included in the data (2007–2013: coefficient estimate = 0.0007, z_{508} = 0.13, $p = 0.90$).

Temperature data and comparisons between nest types

I collected three sets of data at different times throughout the year to compare various nest types. Three sets of experiments were conducted because initially there were not enough temperature recorders available for use. As more became available, it was possible to test more nest types simultaneously. This is not ideal as mean ambient temperature varied for each experiment, making it difficult to compare between the groups.

The first dataset compared artificial burrows, nest boxes, and surface nests. I carried out 7 replicates giving a total of 54 days of data—the mean ambient temperature over this period was 27.3°C.

Using multiple pairwise comparisons, I found that maximum temperatures in artificial burrows (coefficient estimate = 10.77, z_{24} = 5.46, $p < 0.001$) and nest boxes (coefficient estimate = 7.61, z_{24} = 3.86, $p < 0.001$) were significantly cooler than at surface nests (Figure 3.15). There were no significant differences among artificial burrows, nest boxes, and ambient temperatures, although the mean maximum temperature estimated for nest boxes was about 3°C higher.

The temperature amplitude was smaller within artificial burrows (coefficient estimate = 14.46, z_{24} = 7.39, $p < 0.001$) and nest boxes (coefficient estimate = 8.80, z_{24} = 4.50, $p < 0.001$) than it was for surface nests (Figure 3.16). However, the amplitude also differed significantly between the two artificial nest types, being lower in artificial burrows than nest boxes (coefficient estimate = 5.66, z_{24} = 2.89, $p = 0.02$).

Temperatures recorded inside artificial burrows exceeded 30°C for the least amount of time during the sampling period. The temperature within artificial burrows was above 30°C for approximately 1.9% of the time while the ambient temperature was above 30°C for 2% of the time. Inside nest boxes this rose to 4.2% of the time and in surface nests the temperature exceeded 30°C for 7.6% of the time (Figure 3.17). The amount of time temperatures recorded above 25°C showed a similar pattern.

The second dataset compared artificial burrows, nest boxes, vegetation nests, and surface nests. I carried out 4 replicates, giving a total of 12 days of data—the mean ambient temperature over this period was 33.2°C.

I found that temperature was significantly higher inside artificial burrows (coefficient estimate = -6.93, $z_{15} = -3.87$, $p = 0.001$) and nest boxes (coefficient estimate = -6.99, $z_{15} = -3.90$, $p < 0.001$) than in vegetation nests (Figure 3.18). The temperature amplitude inside vegetation nests was smaller than surface nests (coefficient estimate = -17.52, $z_{15} = -10.02$, $p < 0.001$) and nest boxes (coefficient estimate = -7.27, $z_{15} = -4.16$, $p < 0.001$), but did not differ significantly from artificial burrows (coefficient estimate = -4.41, $z_{15} = -2.52$, $p = 0.09$). Temperature amplitude was also smaller in artificial burrows (coefficient estimate = 13.11, $z_{15} = 7.50$, $p < 0.001$) and nest boxes (coefficient estimate = 10.25, $z_{15} = 5.86$, $p < 0.001$) compared to surface nests (Figure 3.19).

The least amount of time temperatures were recorded at above 30°C was in vegetation nests (5.1%). Ambient temperature was above 30°C for 15.4% of the time, while the temperature was above 30°C for 21.3% of the time inside artificial burrows, and for 28.6% of the time inside nest boxes. For surface nests the temperature exceeded 30°C for 39.5% of the time (Figure 3.20). The result was less pronounced for temperatures above 25°C, but still had the same trend.

The third dataset compared nest boxes and vegetation nests only. I carried out 6 replicates to give a total of 56 days of data—the mean ambient temperature over this period was 28.7°C.

Ambient temperature was above 30°C for 7.2% of the time, while the temperature inside nest boxes was above 30°C for 10.7% of the time, and the temperature inside vegetation nests was above 30°C for 2.3% of the time. Overall, however, this data set produced no significant results.

Orientation and temperatures in nest boxes

Orientation of nest boxes had a significant effect on the amount of time temperatures within the nest boxes exceeded 30°C ($\chi^2 = 185.24$, df = 4, $p < 0.001$; Figure 3.21), with North and

East orientations having the longest exposure to temperatures above 30°C. The temperature inside nest boxes at all orientations was significantly higher than the ambient temperature.

Long-term trends in weather at Robben Island

I used long-term weather data to assess whether African penguins on Robben Island have been experiencing increases in temperature and rainfall in recent years, specifically during the first few months of the breeding season. Total monthly rainfall from 1950–2012 showed a significant decrease ($t_{(60)} = -2.08$, $p = 0.04$; Figure 3.22) during the combined months of February, March and April. Daily maximum temperature records from 1975–2012 showed a significant increase ($t_{(37)} = 2.15$, $p = 0.04$; Figure 3.23) in the number of days where temperatures recorded above 30°C during the combined months of February, March and April.

Discussion

Artificial nests improve breeding productivity (Kemper *et al.* 2007a, Sherley *et al.* 2012b), and are thought to be able to protect from climatic conditions. High temperatures and flooding may lead to breeding failure, and it is thought that artificial nests may be able to reduce exposure of breeding birds to extreme heat and rainfall. In this study, I found that weather events, such as rainfall and temperature, had a significant effect on nest failure which differed depending on the breeding stage of the nest. Incubation was affected by rain, whereas chick rearing was affected by rain and temperatures (Figure 3.9, 3.13, 3.14). Nest failure for all nests was affected by weather, but there were only minor differences between nest types, with the exception of incubation in nest boxes (Figure 3.10, 3.11).

Increases in rainfall resulted in an increase in the number of incubating nests that failed, but it did not differ based on nest type. It is likely that all nests could be affected by flooding to some degree. However, for the years when there were artificial burrows, this effect was no longer apparent. This could be due to artificial burrows providing better protection from flooding, and thus decreasing the risk of nest failure when it rains or due to a lack of power as the data set was smaller (seven vs 13 years) with artificial burrows included.

Nest failure during incubation did differ amongst nest types when temperature was a factor, for both analyses with and without artificial burrows. Surface nests and natural burrows exhibited the highest rates of incubation failure. Natural burrows have a constant microclimate (Frost *et al.* 1976a) and have been thought to be adequate in protecting breeding birds from high temperatures. It is possible that this high incidence of nest failure could be due to the sandy substrate on Robben Island making them more prone to collapse (Frost *et al.* 1976a, Sherley *et al.* 2012b). Nest boxes were the only nest type to display a decreasing trend in failure as temperatures increased. This could perhaps be an artefact of a smaller sample size.

Chick mortality was affected by temperature in both time period analyses (2001–2013 and 2007–2013), whereas rain only had an effect in the 2001–2013 analysis and not during 2007–2013 when artificial burrows were included in the analysis. This could be because of the smaller sample size, perhaps artificial burrows are not as susceptible to heavy rains or most of the heavy rainfall events occurred in the earlier years of the dataset (2001–2006). Chicks, especially when they are older, are better able to withstand extreme environmental conditions (Kemper *et al.* 2007a). Young chicks are not able to thermoregulate properly and would be more vulnerable to changing temperatures (Erasmus and Smith 1974). Chick size may thus be a factor; mortality may be greater when the chicks are smaller. The size of the brood may also play a role, it is more energetically demanding to raise a two-chick brood, and may lead to a greater chance of whole or partial nest failure. The size of the chick and the size of the brood may be important to consider in any future modelling as they may explain some of the effects within the data.

Nest type had an overall effect on chick mortality. Natural burrows and open nests had the highest rates of mortality and nest boxes, artificial burrows, and buildings had the lowest rate. These results resemble those of Sherley *et al.* (2012b) who found that artificial nests (nest boxes and artificial burrows combined) and buildings had the highest proportion of chicks fledging, and vegetation nests had the lowest proportion of chicks fledging. In this study, however, I found that open nests and natural burrows had a greater mortality rate than vegetation nests.

From the operative temperatures recorded within the various nest types, the lowest maximum temperature was for ambient temperature, while surface temperatures were highest, with mean maximum temperatures exceeding 35°C and 45°C in the two sampling groups in which surface temperatures were measured (the corresponding mean ambient temperatures were 27.3°C and 33.2°C respectively). Surface nests provide no protection from the sun and would direct expose a breeding bird to solar radiation (Frost *et al.* 1976a). Solar radiation is more likely to cause heat stress than high ambient temperatures (Randall 1983).

Artificial nests provide some protection from solar radiation, similar to burrow nests (Frost *et al.* 1976a), and would be cooler for a breeding bird than nesting out in the open. Artificial fibreglass burrows recorded lower maximum daily temperatures than wooden nest boxes, and this may be because they are mostly buried under the surface and would better mimic a natural burrow, rather than if they were just placed on the surface (as in Lei *et al*. 2014). Nest boxes, on the other hand, are placed on the surface, usually without any extra cover. Nest boxes used by little penguins had higher temperatures than surrounding vegetation, with poor ventilation being cited as the cause (Ropert-Coudert *et al.* 2004). Lei *et al.* (2014) found that artificial nests made of cement had cooler temperatures than fibreglass burrows, and this is thought to be due to better ventilation; the cement burrows had openings on both sides to allow for air flow. Fibreglass burrows are translucent; if they are placed on the surface or only partially buried, they will still be exposed to solar radiation.

The artificial burrows on Robben Island were initially buried and covered with soil and rocks, but over time strong winds and rain varied the degree of cover for each artificial burrow (Sherley *et al.* 2012b). It is possible that the artificial burrows that are partially exposed may experience hotter temperatures than those that better mimic natural burrows by being completely covered. Lei *et al.* (2014), however, found no significant difference in internal temperatures of fibreglass burrows by adding shade cover through the use of vegetation or other means.

Artificial burrows experienced lower ranges in temperature of approximately 10°C compared to 15°C for nest boxes. Lei *et al.* (2014) recorded fibreglass burrows to have a temperature range of about 12°C, and they found natural burrows to have a range of 6°C. Natural burrows experience a more constant climate by having higher relative humidity, less fluctuation in air temperature, protection from direct sun exposure, and no wind effect (Frost *et al.* 1976a). Surface nests had a large range in temperature (25°C) because they are exposed to higher temperatures through solar radiation. Artificial nests seem able to maintain a more constant climate, but still not to the same degree as natural burrows.

Seabirds have a thermal limit and when temperatures go above that, they will become heat stressed with potential adverse effects (Oswald and Arnold 2012). The thermal limit for African penguins is unknown, but Frost *et al.* (1976a) observed thermoregulatory behaviours once ambient temperatures exceeded 28°C, and the heat stress point of the related Humboldt penguin is 30°C (Drent and Stonehouse 1971). The length of time that nest temperatures remain at this high level could determine the survival of the nest. An adult is more likely to abandon if it is consistently exposed to temperatures that require an increase in thermoregulation to tolerate.

Nests on the surface have the most sun exposure, and had the highest proportion of temperatures above 30°C. This is in contrast to the findings of Lei *et al.* (2014) who found that artificial fibreglass burrows had the highest proportion of temperatures above 30°C out of all nest types, including those on the surface. The study by Lei *et al.* (2014) did not use operative temperature models to account for solar radiation effects and the substrate at Bird Island, where their study was conducted, makes it difficult to fully bury the artificial burrows. Artificial nests in this study were not able to prevent temperatures from exceeding 30°C and thus breeding penguins could still experience uncomfortably high temperatures on hot days within these nests. Frost *et al.* (1976a) reported African penguins in the field already exhibiting heat stress behaviours once ambient temperatures reached above 24°C, suggesting that penguins may start to feel the heat far below a calculated heat stress point.

The majority of breeding African penguins on Robben Island nest under vegetation. Extensive vegetation, especially during the dry summer months, presents a fire risk. Robben Island managing authorities have been implementing an ongoing management plan for the removal of alien vegetative species and the cutting of fire breaks (Robben Island Museum 2013). This was the original motivation behind the introduction of artificial nests on the island (Sherley *et al.* 2012b), as most African penguins nested under alien vegetation (Crawford *et al.* 1995) and these would provide an alternative form of shelter. It is thus important to test whether these artificial nests provide a sufficient microclimate to replace nests under vegetation.

In this study, temperatures recorded inside artificial nests were lower than the temperatures that were recorded on the surface, but they still remained higher than the temperatures that were recorded in nests under vegetation. This may be because nests under vegetation provide shade, while still allowing for cooling breezes that neither the artificial burrows nor the nest boxes might experience. The types of vegetation and the degree of cover they provide can vary greatly, and it is likely that not all vegetation nests experience the same conditions. This study tested only under rooikrans with partial and complete shade cover. A small number of replicates were taken for nests under vegetation and it would be beneficial to take more samples of vegetation and artificial nests at the same time to see if degree of vegetation cover could make a difference in the temperatures recorded.

Sherley *et al.* (2012b) studied the effect of nest types on breeding productivity and found that artificial nests (fibreglass burrows and nest boxes combined) had greater breeding success than vegetation nests. In this study I obtained similar results by finding that artificial nests had a lower rate of nest failure than vegetation nests. This is in contradiction to the nest temperature findings if we assume that increased temperatures lead to breeding failure. This suggests that other factors affecting artificial nests could be involved, such as the ability to protect from flooding and predation, and even the quality of the individual.

The orientation of nest boxes determined the proportion of time temperatures recorded above 30°C within the nests. For this study, I did not test the effect of orientation on egg or chick mortality so it is not known whether placement of nest boxes would have an effect on nest survival. Other studies have found variations in temperatures within nest boxes at different orientations, yet they reported no effects on nest survival (Butler *et al.* 2009, Catry *et al.* 2011). Frere *et al.* (1992) reported no effect on internal temperature, and suspected that the nature and topography of the nests may void any possible effects of orientation on nest survival.

Models suggest that the global mean temperature will increase by 2050, compared to 1961–1990 (Rowlands *et al.* 2012). During the period of 1962–2009, South Africa was found to have undergone general warming. In the western part of South Africa, there's been an increasing trend of extreme maximum temperatures (Kruger and Sekele 2013). New *et al.* (2006) also reported that southern Africa and other regions are showing signs of warming based on temperature extremes; the frequency of hot days and nights has increased. Areas in South Africa, including the south western region, have also displayed an increase in the amount of days per year that experience greater and more extreme rainfall (Kruger 2006, New *et al.* 2006). Models predicting the responses of southern African birds to climate change show that 62% of bird species may lose climatically suitable habitat (Coetzee *et al.* 2009). If these areas are reduced it could threaten southern African birds that are unable to cope with changing resources and geographical shifts (Simmons *et al.* 2004).

African penguins on Robben Island start breeding around the end of the austral summer, with incubation usually ranging from February to April. These months have shown an increase in maximum temperatures that exceed 30°C within the last 40 years, and rainfall has decreased. If this pattern of increasing temperature continues, it may be detrimental to the successful breeding of African penguins on Robben Island.

In this study I found that artificial nests were the least vulnerable to nest failure during both incubation and chick rearing, yet they experienced higher temperatures than vegetation nests. This suggests that they may not represent the optimal breeding habitat for African penguins, but also that they are far from detrimental, and provide adequate substitute habitat if vegetation must be removed. Monitoring the life history of individuals using artificial nests could help in determining any effects on future survival, but as it stands, artificial nests are not an ecological trap and are a better alternative than nesting on the surface. Future work on design and placement of artificial nests would further benefit the conservation of African penguins on Robben Island.

Figure 3.1 An example of a nest under vegetation, occupied by a breeding African penguin *Spheniscus demersus* on Robben Island.

Figure 3.2 An example of an African penguin *Spheniscus demersus* nest inside a disused building on Robben Island.

Figure 3.3 A wooden A-frame nest box placed beside an artificial fibreglass burrow at an African penguin *Spheniscus demersus* nesting area on Robben Island. A painted copper sphere containing an iButton for recording operative temperature can be seen inside the nest box.

Figure 3.4 Artificial fibreglass burrows used by nesting African penguins *Spheniscus demersus* on Robben Island, with (a) partial cover and (b) complete cover.

Figure 3.5 A copper sphere, painted to resemble the dorsal and ventral surfaces of an African penguin *Spheniscus demersus*, containing an iBsutton is placed on the surface to record operative temperature. A Stevenson screen containing an iButton is placed on the surface to record ambient temperature.

Figure 3.6 Four wooden nest boxes set up at the orientations of North, East, South, and West. Each nest box contained a painted copper sphere to record operative temperature, and a Stevenson screen was placed in the open to record ambient temperature.

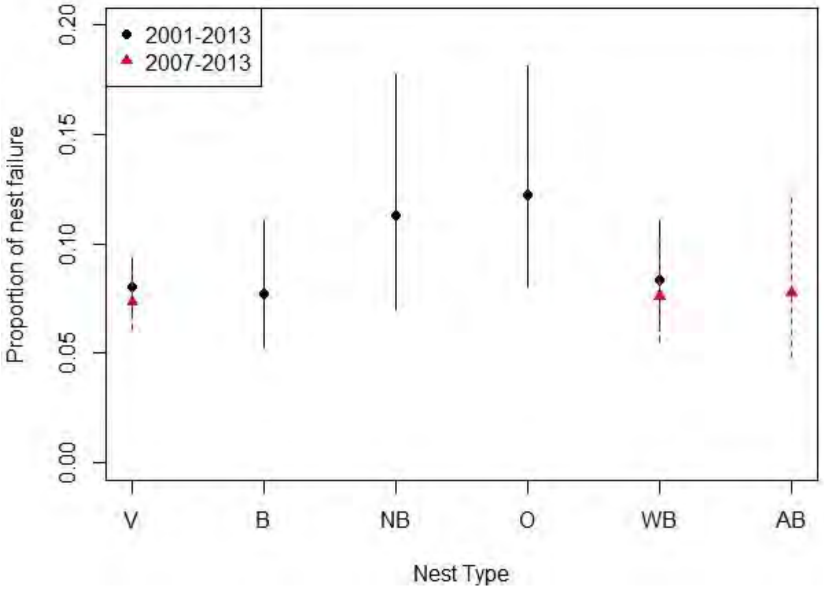

Figure 3.7 The estimate of nest failure for African penguin nests *Spheniscus demersus* at the incubation stage as a function of nest type, with rainfall and temperature data held at their means. The nest types include vegetation (V), building (B), natural burrow (NB), open (O), and nest box (WB) for 2001–2013 (circle, n = 781). Data for 2007–2013 (triangle, n = 420) included artificial burrows (AB) and they were compared with vegetation nests (V) and nest boxes (WB). The vertical lines represent the 95% confidence intervals.

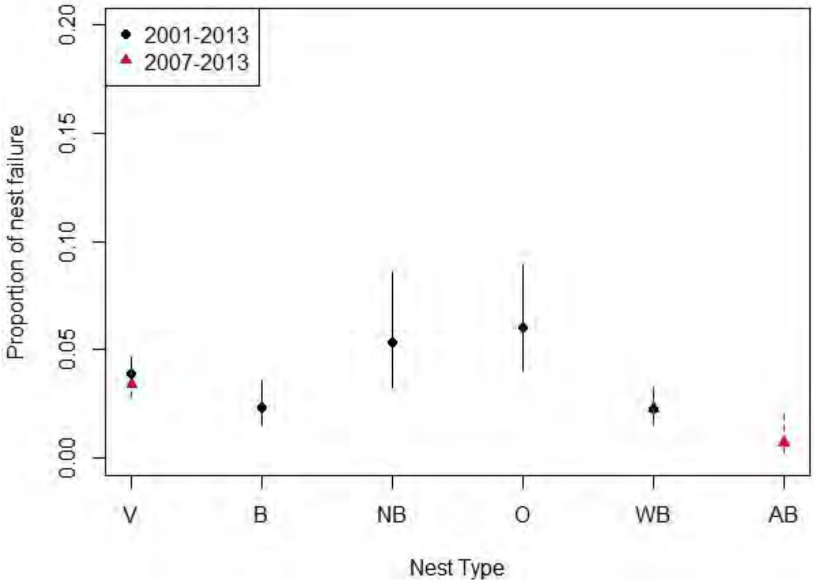

Figure 3.8 The estimate of nest failure for African penguin nests *Spheniscus demersus* at the chick-rearing stage as a function of nest type, with rainfall and temperature data held at their means. The nest types include vegetation (V), building (B), natural burrow (NB), open (O), and nest box (WB) for 2001–2013 (circle, n = 947). Data for 2007–2013 (triangle, n = 514) included artificial burrows (AB) and they were compared with vegetation nests (V) and nest boxes (WB). The vertical lines represent the 95% confidence intervals.

Table 3.1 Selection of the generalized linear mixed-effects models (GLMM) to compare the proportion of nest failures at the incubation stage and the chick-rearing stage of African penguins *Spheniscus demersus* nesting on Robben Island to weather variables and type of nest. The explanatory variables used to create the models were nest type (NT), rainfall (Rain), and maximum temperature (MaxTemp). Models were grouped under two time periods; 2001–2013 and 2007–2013. The model with the best fit (bold) was selected based on the lowest Akaike's information criterion (AICc) value, and the Akaike weight (AICc weight) showing the support for each model. The difference from the preferred model (ΔAICc) and the number of parameters (K) are also shown.

Model	Predictors	K	AICc value	ΔAICc	AICc weight
Incubation (2001–2013)					
2	**NT + Rain + MaxTemp + NT*MaxTemp**	**12**	**1429.8**	**0**	**0.947**
1	NT + Rain + Max Temp + NT*Rain + NT*MaxTemp	16	1436.6	6.8	0.031
3	NT + Rain + MaxTemp	8	1437.3	7.5	0.022
Incubation (2007–2013)					
2	**NT + Rain + MaxTemp + NT*MaxTemp**	**8**	**891.9**	**0**	**0.654**
1	NT + Rain + Max Temp + NT*Rain + NT*MaxTemp	10	893.4	1.5	0.302
3	NT + Rain + MaxTemp	6	897.3	5.4	0.044
Chick-rearing (2001–2013)					
3	**NT + Rain + MaxTemp**	**8**	**1380.9**	**0**	**0.885**
2	NT + Rain + MaxTemp + NT*MaxTemp	12	1385.1	4.2	0.110
1	NT + Rain + Max Temp + NT*Rain + NT*MaxTemp	16	1391.1	10.2	0.0055
Chick-rearing (2007–2013)					
3	**NT + Rain + MaxTemp**	**6**	**775.8**	**0**	**0.67**
1	NT + Rain + Max Temp + NT*Rain + NT*MaxTemp	10	778.2	2.3	0.21
2	NT + Rain + MaxTemp + NT*MaxTemp	8	779.3	3.4	0.12

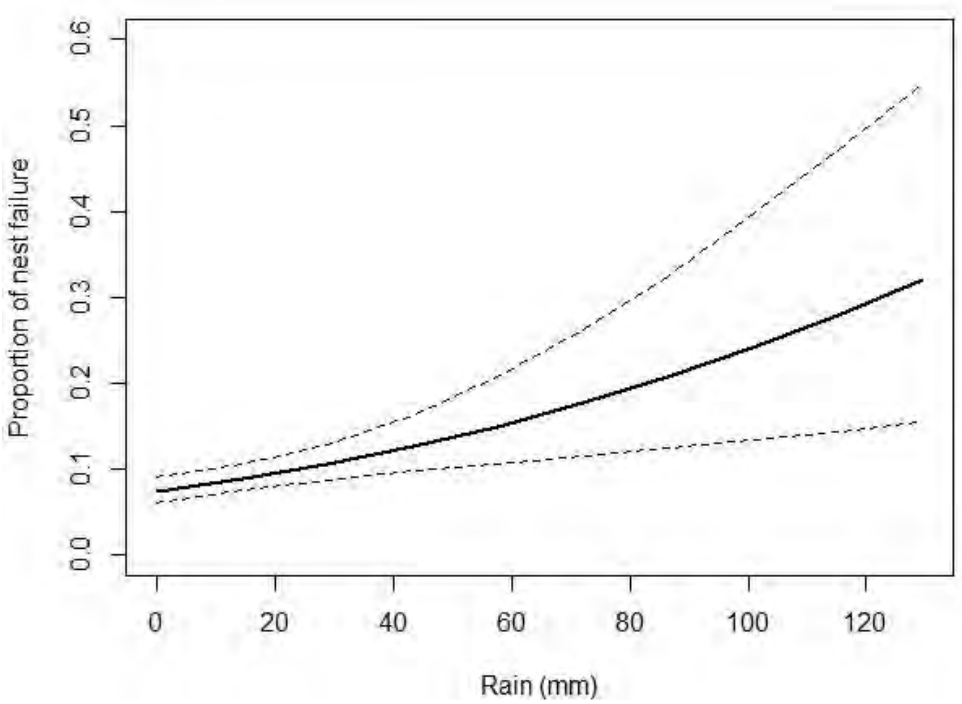

Figure 3.9 The proportion of nest failures as a function of rainfall during incubation, incorporating five types of African penguin *Spheniscus demersus* nests on Robben Island: vegetation, building, natural burrow, open, and nest box. The data were collected from 2001–2013 (n = 781). The solid line is the predicted fit from the best supported GLMM and the dashed lines represent the 95% confidence intervals.

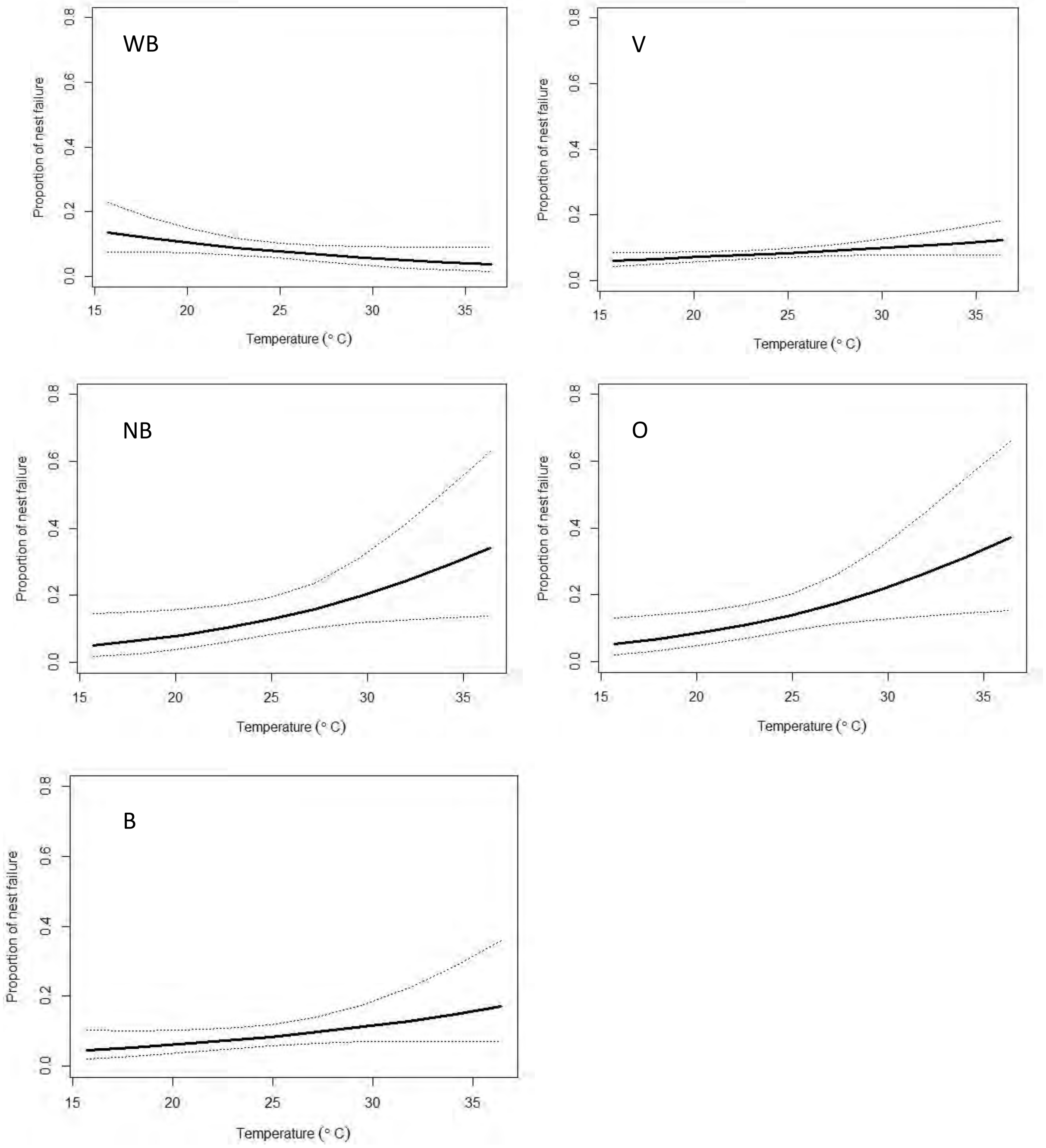

Figure 3.10 The proportion of nest failures of African penguins nests *Spheniscus demersus* at the incubation stage, separated by nest types, as a function of maximum temperature on Robben Island from 2001–2013 (n = 781). The nest types are: vegetation nests (V), buildings (B), natural burrows (NB), open nests (O), and nest boxes (WB). The solid lines are the predicted fit from the best supported GLMM and the dashed lines represent 95% confidence intervals.

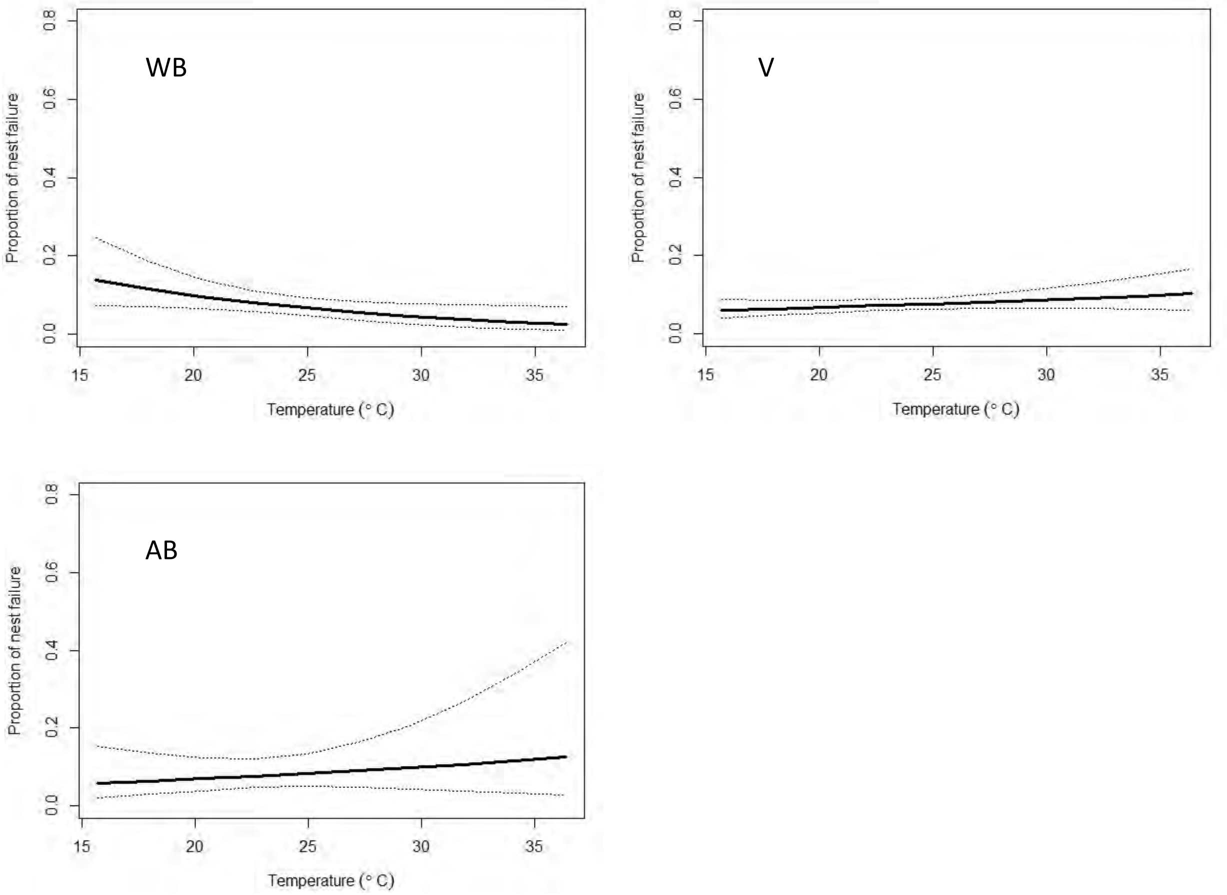

Figure 3.11 The proportion of nest failures of African penguins nests *Spheniscus demersus* at the chick-rearing stage, separated by nest types, as a function of maximum temperature on Robben Island from 2007–2013 (n = 514). Artificial burrows (AB) were compared to vegetation nests (V) and nest boxes (WB). The solid lines are the predicted fit from the best supported GLMM and the dashed lines represent 95% confidence intervals.

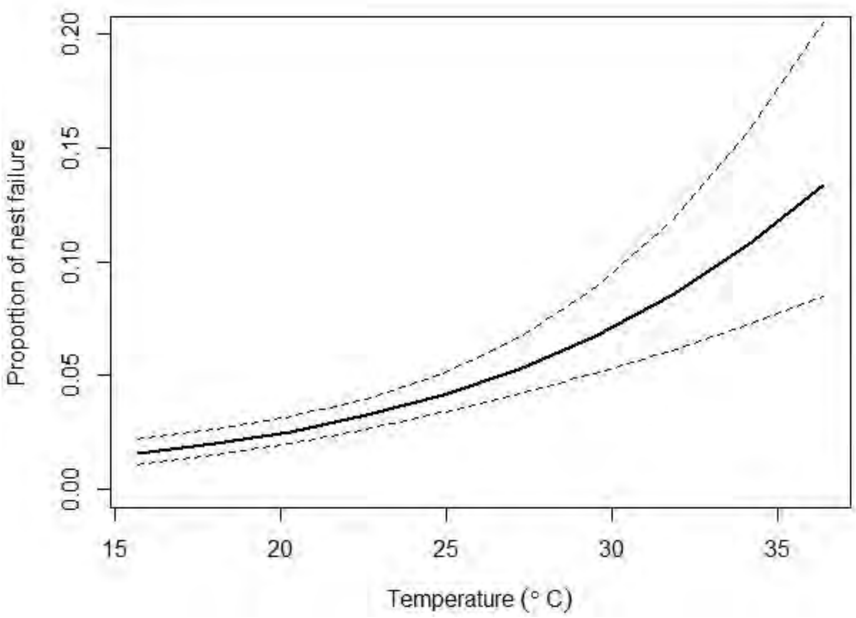

Figure 3.12 The proportion of nest failures as a function of maximum temperature during the chick-rearing stage, incorporating five types of African penguin *Spheniscus demersus* nests on Robben Island: vegetation, building, natural burrow, open, and nest box. The data were collected from 2001–2013 (n = 947). The solid line is the predicted fit from the best supported GLMM and the dashed lines represent the 95% confidence intervals.

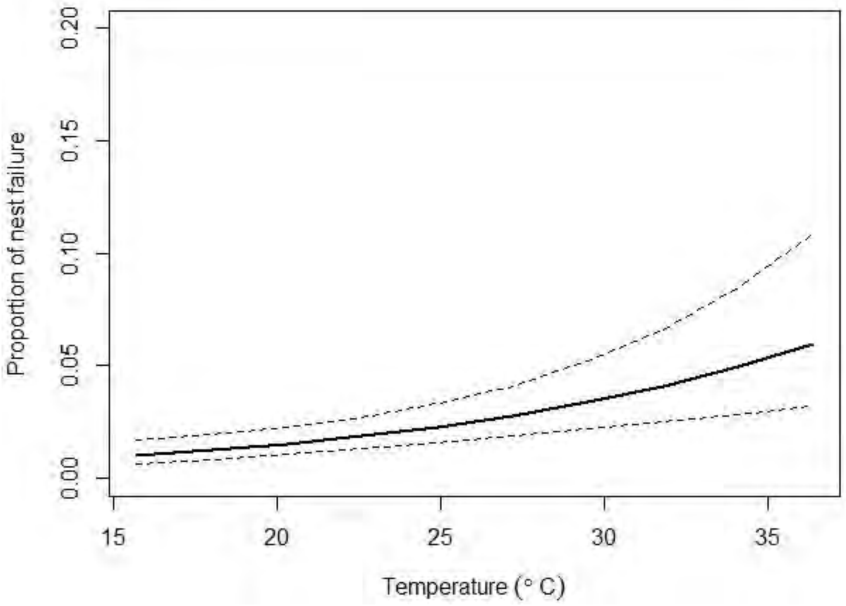

Figure 3.13 The proportion of nest failures as a function of maximum temperature during the chick-rearing stage, incorporating three types of African penguin *Spheniscus demersus* nests on Robben Island: vegetation, nest box, and artificial burrow. The data were collected from 2007–2013 (n = 514). The solid line is the predicted fit from the best supported GLMM and the dashed lines represent the 95% confidence intervals.

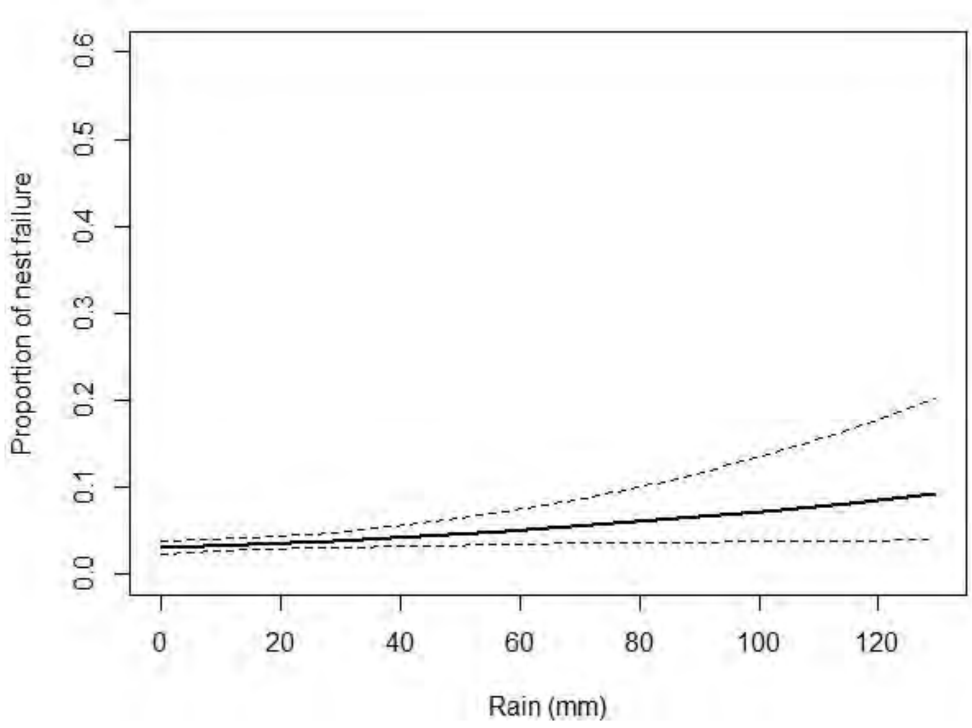

Figure 3.14 The proportion of nest failures as a function of rainfall during the chick-rearing stage, incorporating five types of African penguin nests on Robben Island: vegetation, building, natural burrow, open, and nest box. The data were collected from 2001–2013 (n = 947). The solid line is the predicted fit from the best supported GLMM and the dashed lines represent the 95% confidence intervals.

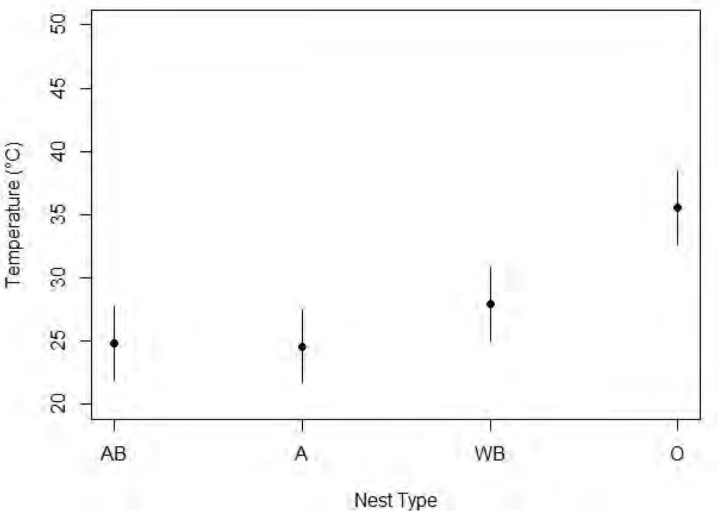

Figure 3.15 The estimated mean maximum daily temperature from 54 days of sampling and 7 replicates (n = 216), with a mean ambient temperature of 27.3°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

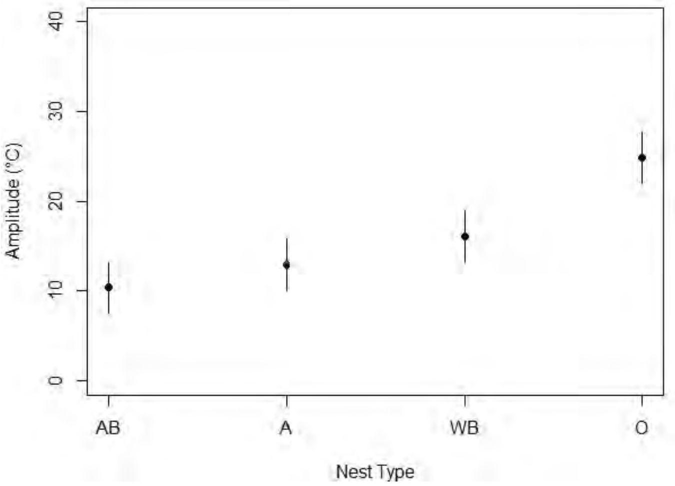

Figure 3.16 The estimated mean range in temperature (amplitude) from 54 days of sampling and 7 replicates (n = 216), with a mean ambient temperature of 27.3°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

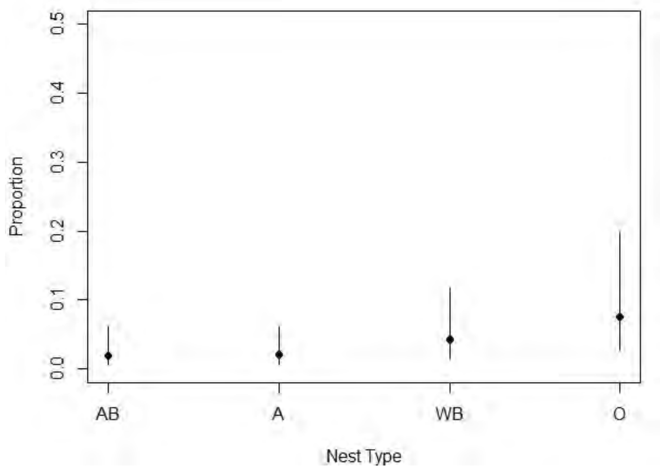

Figure 3.17 The estimated mean proportion of maximum temperatures that recorded above 30°C from 54 days of sampling and 7 replicates (n = 216), with a mean ambient temperature of 27.3°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

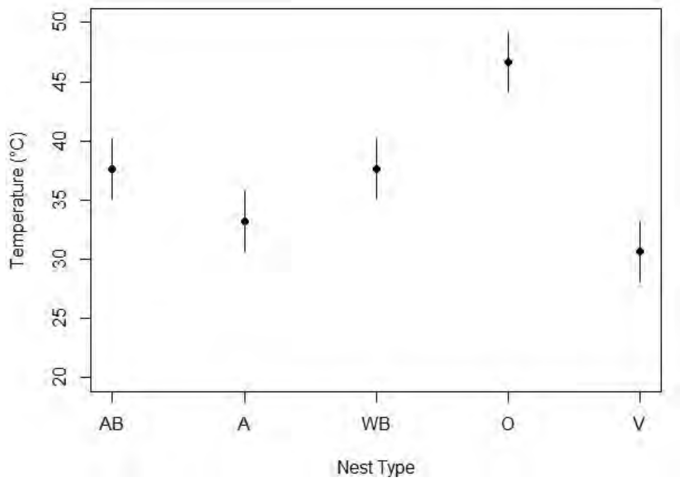

Figure 3.18 The estimated mean maximum daily temperature from 14 days of sampling and 4 replicates (n = 60), with a mean ambient temperature of 33.2°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), vegetation nests (V), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

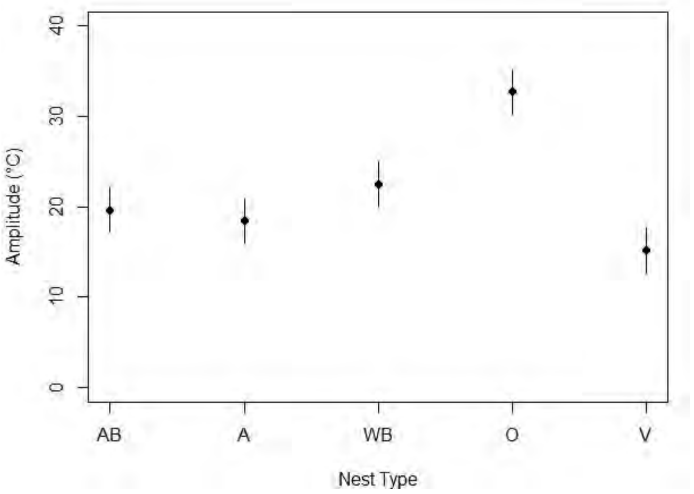

Figure 3.19 The estimated mean range in temperature (amplitude) from 12 days of sampling and 4 replicates (n = 60), with a mean ambient temperature of 33.2°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), vegetation nests (V), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

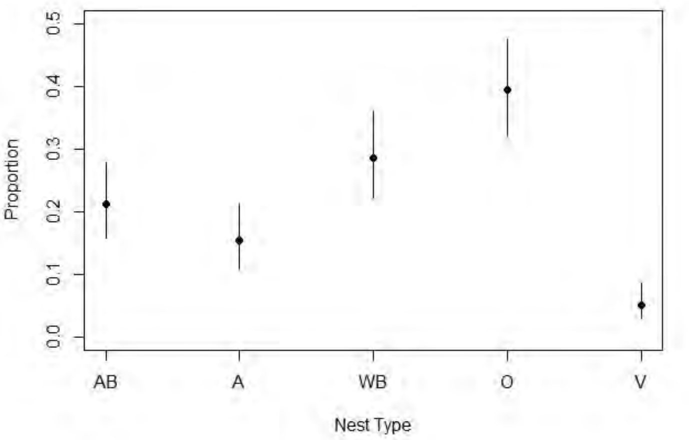

Figure 3.20 The estimated mean proportion of maximum temperatures that recorded above 30°C from 12 days of sampling and 4 replicate (n = 60), with a mean ambient temperature of 33.2°C. The vertical lines represent the 95% confidence intervals. Operative temperatures were recorded inside African penguin *Spheniscus demersus* nests using painted copper spheres containing iButtons. The nests included artificial burrows (AB), nest boxes (WB), vegetation nests (V), and surface nests (O). A Stevenson screen containing an iButton recorded ambient temperature (A).

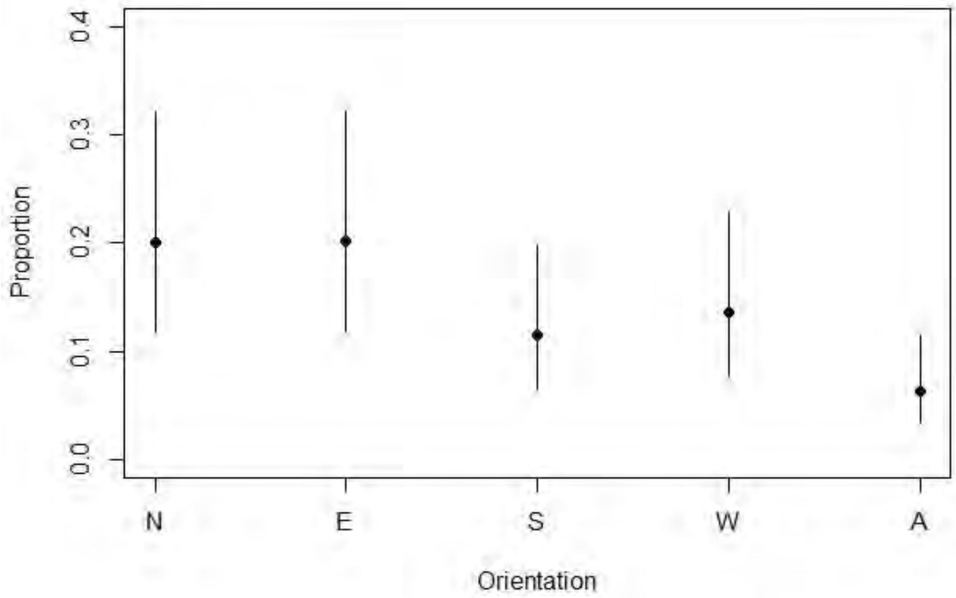

Figure 3.21 The estimated mean proportion of temperatures exceeding 30°C (n = 7335). The vertical lines represent the 95% confidence intervals Nest boxes were placed at the orientations of North (N), East (E), South (S) and West (W). Operative temperature was recorded in each nest box, and ambient temperature (A) was also recorded.

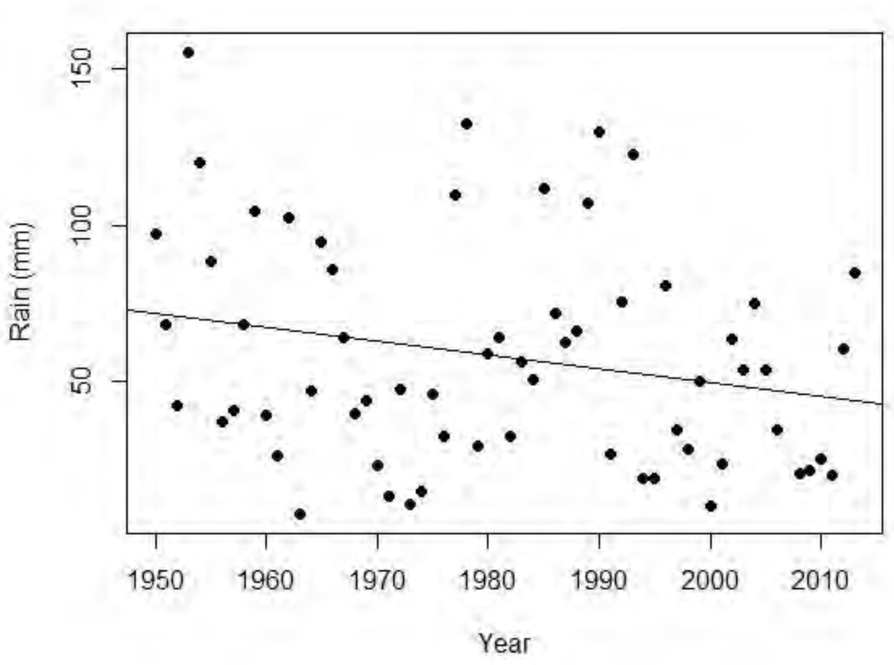

Figure 3.22 Linear fit of total monthly rainfall data for the combined months of February, March, and April from 1950–2012 (n = 62). Long-term rainfall data was obtained from the South African Weather Service station on Robben Island.

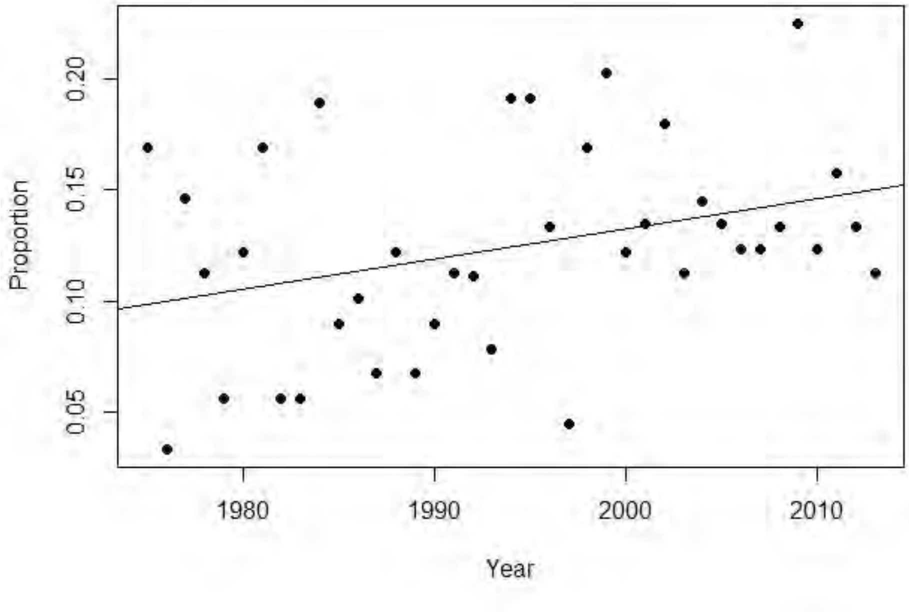

Figure 3.23 Linear fit of the proportion of days in the combined months of February, March, and April where daily maximum temperature exceeded 30°C from 1975–2012 (n = 39). Long-term temperature data was obtained from the South African Weather Service station at Cape Town International Airport and used as a proxy for Robben Island.

Conclusions

African penguins are experiencing a drastic decline; one of the main factors thought to contribute to this decline is the availability of food. African penguins rely on food resources close to the colony throughout the breeding season to ensure successful breeding. Body condition of a seabird can be used to represent changes in their environment, such as food availability. Good body condition throughout breeding has been shown to have a positive effect on breeding success, and it likely that body condition prior to breeding may also have an influence on subsequent breeding success.

There have been studies that have demonstrated a carry-over effect of body condition from the non-breeding season into the subsequent breeding season that resulted in improved breeding success (Harrison *et al.* 2013, Robb *et al.* 2008, Salton *et al.* 2015). The data from Chapter 2 showed that birds with lower mass raised fewer chicks. The mass of the lighter adult had a larger effect, suggesting that it is important for both breeding adults in a pair to be in good condition. If the mass of the lighter bird of a pair was below 2.0 kg no chicks were fledged. Birds that were heavier managed to raise one chick, while pairs where the lighter bird had an initial mass at the onset of breeding greater than 2.4 kg managed to fledge two chicks. These data indicate that there is evidence of a carry-over effect where mass at the onset of breeding can have a significant influence in the success of a breeding attempt. Of course many other factors, not least local food availability before and during the breeding season will also have impact on breeding success.

A carry-over effect of body mass suggests that African penguins may not just rely on local food availability throughout breeding, but may also build up reserves prior to breeding to ensure a successful breeding attempt. This would highlight the importance of food availability not just at a local level, but also at a regional level.

Robben Island is starting to implement a management plan for the removal of alien vegetation and the cutting of vegetation to create fire breaks. This has resulted in the loss of some of the nesting habitat used by breeding African penguins. Artificial nests have been put in place to provide alternative nesting sites. It is, however, important that these nests don’t cause a negative impact on the population. Due to the lack of marked African penguins it is difficult to monitor any long term effects on the survival of adults who use artificial nests. It is possible that although breeding attempts are successful, an adult might expend more energy than it would otherwise because of the conditions, such as increased temperature, experienced in these nests, compromising its future survival. However, because of the low failure rates found in this study and the increased breeding productivity found in Sherley *et al.* (2012b), artificial nests are not considered an ecological trap and can be a suitable nesting alternative on Robben Island.

Artificial nests on Robben Island do not protect penguins from experiencing high temperatures on hot days, but they are a better alternative than nesting on the surface. They provide shade which protects the penguin from solar radiation, and they likely provide some protection from predators and storms. South and West facing nest boxes experienced cooler temperatures than ones that faced North or East. This difference in temperature between orientations of nest boxes suggests that placement of artificial nests is an important consideration.

Vegetation nests experience the coolest temperatures on hot days but they still have higher failure rates than artificial nests. This means that other factors may be involved such as exposure to rain and flooding, predation, parasites, or even the individual quality of adults occupying various nest types.

Global temperatures are predicted to increase (IPCC 2014) and long term weather data near Robben Island is showing an increasing trend in the amount of days where temperatures are exceeding 30°C during the first few months of the breeding season. This highlights the importance of adequate nesting habitat to protect African penguins from rising temperatures in their environment.

It has been shown that both body mass before breeding and variability in climate can have an impact on breeding success. An African penguin in good condition may be better able to withstand changes in climatic conditions.

Future Recommendations

The effect of body mass at the onset of breeding was assessed in a preliminary study using a non-invasive technique on Robben Island to measure weights of African penguins at the nest without the need to handle the birds. Because of this only a small sample size was obtained during both years. It is recommended that this study continue so that it may be possible to get larger sample sizes, and to get a longer term data set since there was evidence in this study that there can be year to year variation. It is also recommended to use a body condition index rather body mass alone to account for any size variations among individuals. One of the aims of this study was to be able to obtain measurements without too much interference, in the hopes to mitigate any stress related to handling. A body condition index requires a structural size measurement to relate to body mass. In the case of African penguin chicks, a measurement of head length is used (Lubbe *et al.* 2014). Structural measurements are generally obtained by handling the bird, but it is recommended to test the use of imagery with objects of known size to estimate size measurements to avoid the need for handling.

It is recommended to further monitor the current types of artificial nests for breeding success and to test variations in design and placement to determine an optimal nest site alternative for breeding African penguins. Nest boxes on Robben Island are mostly out in the open with no extra cover. Further tests of nest boxes with some shading through natural or artificial means is recommended to see if it will prevent the nest boxes from reaching higher temperatures. Artificial burrows recorded lower temperatures, likely because they are partially buried allowing for extra cover, but it is recommended to test more that are completely buried to see if will allow them to better mimic the conditions of a natural burrow. It may also be of interest to test the parasite loads experienced between artificial nests and nests in vegetation as a reason for why artificial nests are more successful. This study only conducted a small number of replicates that included vegetation nests and it is recommended to continue recording temperatures in the various nest types to get a clearer idea of the temperatures experienced inside nests, and to test between the various types of vegetation that are used for nesting. For example, *Tetragonia tetragonioidesa* provides more cover and may have better ventilation than the artificial nests.

References

Ardia, D.R., Pérez, J.H., Clotfelter, E.D. 2006. Nest box orientation affects internal temperature and nest site selection by Tree Swallows. Journal of Field Ornithology 77: 339–344.

Arnold, T.W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178.

Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist 32: 194–216.

Bakken, G.S., Santee, W.R., Erskine, D.J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. American Zoologist 25: 933–943.

Ballard, G., Dugger, K.M., Nur, N., Ainley, D. G. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. Marine Ecology Progress Series 405: 287–302.

Barham, P. J., Underhill, L. G., Crawford, R. J. M., and Leshoro, T. M. 2007. Differences in breeding success between African penguins (*Spheniscus demersus*) that were and were not oiled in the MV Treasure oil-spill in 2000. Emu 107: 7–13.

Barnes, K. N. 1998. The Important Bird Areas of Southern Africa. BirdLife South Africa, Johannesburg.

Batianoff, G.N., Naylor, G.C., Olds, J.A., Fechner, N.A., Neldner, V.J. 2010. Climate and vegetation changes at Coringa-Herald National Nature Reserve, Coral Sea Islands, Australia. Pacific Science 64: 73–92.

Boersma, P.D. 1998. Population trends of the Galápagos penguin: impacts of El Niño and La Niña. Condor 100: 245–253.

Boersma, P.D. and Rebstock, G.A. 2014. Climate change increases reproductive failure in Magellanic penguins. PLoS ONE 9: e85602, doi:10.1371/journal.pone.0085602.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, New York.

Butler, M.W., Whitman, B.A., Dufty Jr., A.M. 2009. Nest box temperature and hatching success of American Kestrels varies with nest box orientation. Wilson Journal of Ornithology 121: 778–782.

Cadiou, B., Bioret, F., Chenesseau, D. 2009. Response of breeding European Storm Petrels to habitat change. Journal of Ornithology 151: 317–327.

Campbell, G. 2014. Effects of temperature on gular fluttering and evaporative water loss in four sympatric cormorants in southern Africa. MSc dissertation. University of Cape Town, Cape Town, South Africa.

Catry, I., Franco, A.M.A., Sutherland, W.J. 2011. Adapting conservation efforts to face climate change: modifying nest-site provisioning for lesser kestrels. Biological Conservation 144: 1111–1119.

Chappell, M.A., Morgan, K.R., Bucher, T.L. 1990. Weather, microclimate, and energy costs of thermoregulation for breeding Adélie Penguins. Oecologia 83: 420–426.

Chastel, O., Weimerskirch, H., Jouventin, P. 1995a. Body condition and seabird reproductive performance: a study of three petrel species. Ecology 76: 2240–2246.

Chastel, O., Weimerskirch, H., Jouventin, P. 1995b. Influence of body condition on reproductive decision and reproductive success in the blue petrel. Auk 112: 964–972.

Chaurand, T. and Weimerskirch, H. 1994. The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea*: A previously undescribed strategy of food provisioning in a pelagic seabird. Journal of Animal Ecology 63: 275–282.

Clarke, J.R. 2001. Partitioning of foraging effort in Adélie penguins provisioning chicks at Béchervaise Island, Antarctica. Polar Biology 24: 16–20.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J., Thuiller, W. 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. Global Ecology and Biogeography 18: 701–710.

Crawford, R.J.M., Makhado, A.B., Waller, L.J., Whittington, P.A. 2014. Winners and losers - responses to recent environmental change by South African seabirds that compete with purse-seine fisheries for food. Ostrich 85: 111–117.

Crawford, R. J. M., Altwegg, R., Barham, B.J., Barham, P.J., Durant, J.M., Dyer, B.M., Geldenhuys, D., Makhado, A.B., Pichegru, L., Ryan, P.G., Underhill , L.G., Upfold, L., Visagie, J., Waller, L.J., Whittington, P.A. 2011. Collapse of South Africa's penguins in the early 21st century. African Journal of Marine Science 33: 139–156.

Crawford, R.J.M., Makhado, A.B., Upfold, L., Dyer, B.M. 2008. Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. African Journal of Marine Science 30: 185–188.

Crawford, R. J. M., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., Leshoro, T. M., and Upfold, L. 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. Biological Conservation 132: 119–125.

Crawford, R. J. M., David, J. H. M., Shannon, L. J., Kemper, J., Klages, N. T. W., Roux, J.-P., Underhill, L. G., Ward, V. L., Williams, A. J., Wolfaardt, A. C. 2001. African penguins as predators and prey– coping (or not) with change. South African Journal of Marine Science 23: 435–447.

Crawford, R. J. M. and Dyer, B. M. 2000. Wildlife of Robben Island. Bright Continent Guide 1. Avian Demography Unit, Cape Town.

Crawford, R. J. M., Shannon, L. J., Whittington, P. A. 1999. Population dynamics of the African penguin *Spheniscus demersus* at Robben Island, South Africa. Marine Ornithology 27: 139–147.

Crawford, R. J. M., v D Boonstra, H. G., Dyer, B. M., Upfold, L. 1995. Recolonisation of Robben Island by African penguins, 1983–1992. In: The Penguins: Ecology and Management, P. Dann, I. Norman, P.N. Reilly, eds. Surrey Beatty and Sons, N.S.W. Australia. Pp 333–363.

Crick, H.Q.P. 2004. The impact of climate change on birds. Ibis 146: 48–56.

Cunningham, S.J., Martin, R.O., Hojem, C.L., Hockey, P.A.R. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. PLoS ONE 8: e74613, doi:10.1371/journal.pone.0074613.

Dann, P. and Chambers, L. 2013. Ecological effects of climate change on little penguins *Eudyptula minor* and the potential economic impact on tourism. Climate Research 58: 67–79.

Davis, L.S. 1982. Timing of nest relief and its effect on breeding success in Adelie penguins (*Pygoscelis adeliae*). Condor 84: 178–183.

Dawson, W.R. 1982. Evaporative losses of water by birds. Comparative Biochemical Physiology 71A: 495–509.

Demongin, L., Poisbleau, M., Strange, I.J., Quillfeldt, P. 2010. Effects of severe rains on the mortality of Southern Rockhopper penguin (*Eudyptes chrysocome*) chicks and its impact on breeding success. Ornitologia Neotropical 21: 1–5.

de Villiers, M. 2002. Effect of a storm on breeding African Penguins *Spheniscus demersus* at Foxy Beach, Boulders Penguin Colony, Simon's Town. Bird Numbers 11: 7–9.

Drent, R.H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

Drent, R.H. and Stonehouse, B. 1971. Thermoregulatory responses of the Preuvian penguin, *Spheniscus humboldti*. Comparative Biochemistry and Physiology Part A 40: 689–710.

Durant, J.M., Crawford, R.J.M., Wolfaardt, A.C., Agenbag, K., Visagie, J., Upfold, L., Stenseth, N.C. 2010. Influence of feeding conditions on breeding of African penguins- importance of adequate local food supplies. Marine Ecology Progress Series 420: 263–271.

Durant, J.M., Anker-Nilssen, T., Chr. Stenseth, N. 2003. Trophic interactions under climate fluctuations: the Atlantic puffin as an example. The Royal Society 270: 1461–1466.

du Toit, M., Underhill, L.G., Crawford, R.J.M. 2004. African penguin populations in the Western Cape, South Africa, 1992–2003. Avian Demography Unit, University of Cape Town, South Africa.

du Toit, M., Boere, G. C., Cooper, J., de Villiers, M. S., Kemper, J., Lenten, B., Petersen, S. L., Simmons, R. E., Underhill, L. G., Whittington, P. A., and Byers, O. P. 2003. Conservation Assessment and Management Plan for Southern African Coastal Seabirds. Cape Town: Avian Demography Unit and Apple Valley: Conservation Breeding Specialist Group.

Erasmus, T. and Smith, D. 1974. Temperature regulation of young jackass penguins, *Spheniscus demersus*. Zoologica Africana 9: 195–203.

Erikstad, K.E., Asheim, M., Fauchald, P., Dahlhaug, L., Tveraa, T. 1997. Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. Behavioral Ecology and Sociobiology 40: 95–100.

Forcada, J. and Trathan, P.N. 2009. Penguin responses to climate change in the Southern Ocean. Global Change Biology 15: 1618–1630

Frere, E., Gandini, P., Boersma, D. 1998. The breeding ecology of Magellanic penguins at Cabo Vírgenes, Argentina: What factors determine reproductive success? Colonial Waterbirds 21: 205–210.

Frere, E., Gandini, P., Boersma, P.D. 1992. Effects of nest type and location on reproductive success of the magellanic penguin *Spheniscus magellanicus*. Marine Ornithology 20: 1–6.

Frost, P.G.H., Siegfried, W.R., Burger, A.E. 1976a. Behavioural adaptations of the jackass penguin, *Spheniscus demersus* to a hot, arid environment. Journal of Zoology 179: 165–187.

Frost, P.G.H., Siegfried, W.R., Copper, J. 1976b. Conservation of the jackass penguin (*Spheniscus demersus* (L.)). Biological Conservation 9: 79–99.

Gaston, A.J. and Hipfner, J.M. 2006. Adult Brünnich's Guillemots *Uria lomvia* balance body condition and investment in chick growth. Ibis 148: 106–113.

Gaston, A.J., Gilchrist, H.G., Hipfner, J.M. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). Journal of Animal Ecology 74: 832–841.

Golet, G.H. and Irons, D.B. 1999. Raising young reduces body condition and fat stores in black-legged kittiwakes. Oecologia 120: 530–538.

Golet, G.H., Irons, D.B., Estes, J.A. 1998. Survival costs of chick rearing in Black-Legged Kittiwakes. Journal of Animal Ecology 67: 827–841.

Hamer, K.C., Schreiber, E.A., Burger, J. 2002. Breeding biology, life histories, and life history-environment interactions in seabirds. In: Biology of Marine Birds, E. A. Schreiber and J. Burger, eds. CRC Press, Boca Raton, FL. Pp 217–262.

Hand, J.L., Hunt, Jr., G.L., Warner, M. 1981. Thermal stress and predation: influences on the structure of a gull colony and possibly on breeding distributions. The Condor 83: 193–203.

Harding, A. M.A., Kitaysky, A.S., Hall, M.E., Welcker, J., Karnovsky, N.J., Talbot, S.L., Hamer, K.C., Grémillet, D. 2009. Flexibility in the parental effort of an Arctic-breeding seabird. Functional Ecology 23: 348–358.

Harrison, X.A., Hodgson, D.J., Inger, R., Colhoun, K., Gudmundsson, G.A., McElwaine, G., Tregenza, T., Bearhop, S. 2013. Environment conditions during breeding modify the strength of mass-dependent carry-over effects in a migratory bird. PLoS ONE 8: e77783, doi:10.1371/journal.pone.0077783.

Hockey, P. A. R., Dean, W. R. J., Ryan, P. G., eds. 2005. Roberts- Birds of Southern Africa. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Hood, L.C., Boersma, D., Wingfield, J.C. 1998. The adrenocortical response to stress in incubating Magellanic penguins (*Spheniscus magellanicus*). Auk 115: 76–84.

IPCC. 2014: Summary for Policymakers. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. Pp 1–32.

IUCN. 2014. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Downloaded on 03 September 2014.

Jacobs, S.R., Elliott, K., Guigueno, M.F., Gaston, A.J., Redman, P., Speakman, J.R., Weber, J. 2012. Determining seabird body condition using nonlethal measures. Physiological and Biochemical Zoology 85: 85–95.

Jakubas, D., Gluchowska, M., Wojczulanis-Jakubas, K., Karnovsky, N.J., Keslinka, L., Kidawa, D., Walkusz, W., Boehnke, R., Cisek, M., Kwaśniewski, S., Stempniewicz, L. 2011. Foraging effort does not influence body condition and stress level in little auks. Marine Ecology Progress Series 432: 277–290.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78: 57–66.

Kemper, J., Underhill, L.G., Roux, J-P. 2007a. Artificial burrows for African penguins on Halifax Island, Namibia: do they improve breeding success? In: 'Final Report of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME'. (Ed. S. P. Kirkman) pp. 101–106. Avian Demography Unit, University of Cape Town, Cape Town. Available at: http://web.uct.ac.za/depts/stats/adu/pdf/bclme12_burrows.pdf.

Kemper, J., Underhill, L.G., Roux, J.-P., Bartlett, P.A., Chesselet, Y.J., James, J.A.C., Jones, r., Uhongora, N.-N., Wepener, S. 2007b. Breeding patterns and factors influencing breeding success of African Penguins Spheniscus demersus in Namibia. In: 'Final Report of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME'. (Ed. S. P. Kirkman) pp. 89-99. Avian Demography Unit, University of Cape Town, Cape Town. Available at: http://web.uct.ac.za.depts/stats/adu/pdf/bclme11_penguin_breeding%20 success.pdf.

Kruger, A.C. 2006. Observed trends in daily precipitation indices in South Africa: 1910–2004. International Journal of Climatology 26: 2275–2285.

Kruger, A.C. and Sekele, S.S. 2013. Trends in extreme temperature indices in South Africa: 1962–2009. International Journal of Climatology 33: 661–676.

Labocha, M.K. and Hayes, J.P. 2012. Morphometric indices of body condition in birds: a review. Journal of Ornithology 153: 1–22.

Lei, B.R., Green, J.A., Pichegru, L. 2014. Extreme microclimate conditions in artificial nests for Endangered African Penguins. Bird Conservation International 24: 201–213.

Libois, E., Gimenez, O., Oro, D., M Mínguez, E., Pradel, R., Sanz-Aguilar, A. 2012. Nest boxes: a successful management tool for the conservation of an endangered seabird. Biological Conservation 155: 39–43.

Lubbe, A., Underhill, L.G., Waller, L.J., Veen, J. 2014. A condition index for African penguin *Spheniscus demersus* chicks. African Journal of Marine Science 36: 143–154.

Lustick, S. 1984. Thermoregulation in adult seabirds. In: Seabird Energetics, G.C. Whittow and H. Rahn, eds. Plenum Press, New York, NY. Pp 183–202.

Meyer, C. 2014. The endangered bank cormorant *Phalacrocorax neglectus*: the heat is on. MSc dissertation. University of Cape Town, Cape Town, South Africa.

Morrison, R.I.G., Davidson, N.C., Wilson, J.R. 2007. Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. Journal of Avian Biology 38: 479–487.

New, M., Hewitson, B., Stephenson, D.B., Tsiga, A., Kruger, A., Manhique, A., Gomez, B., Coelho, C.A.S., Masisi, D.N., Kululanga, E., Mbambalala, E., Bulane, L., Fortunata, L., Mdoka, M.L., Lajoie, R. 2006. Evidence of trends in daily climate extremes over southern and west Africa. Journal of Geophysical Research 111: D14102.

Numata, M., Davis, L.S., Renner, M. 2000. Prolonged foraging trips and egg desertion in little penguins (*Eudyptula minor*). New Zealand Journal of Zoology 27: 277–289.

Oswald, S.A. and Arnold, J.M. 2012. Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. Integrative Zoology 7: 121–136.

Oswald, S.A., Huntley, B., Collingham, Y.C., Russell, D.J.F., Anderson, B.J., Arnold, J.M., Furness, R.W., Hamer, K.C. 2011. Physiological effects of climate on distributions of endothermic species. Journal of Biogeography 38: 430–438.

Paredes, R., Jones, I.L., Boness, D.J. 2005. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped data loggers. Animal Behaviour 69: 197–208.

Parmesan, C. 2006. Ecological and evoluntionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37: 637–669.

Peig, J. and Green, A.J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology 24: 1323–1332.

Peig, J. and Green, A.J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118: 1883–1891.

Pichegru, L. 2013. Increasing breeding success of an endangered penguin: artificial nests or culling predatory gulls? Bird Conservation International 23: 296–308.

Pickering, M. 2012. Project with Bristol Zoo Gardens: Instrumented Nest Boxes for Grey Mouse Lemurs and African Penguins (NPSM17). Final BSc Project. University of Bristol, Bristol, UK.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org.

Randall, R.M. 1983. Biology of the Jackass Penguin *Spheniscus demersus* (L.) at St. Croix Island, South Africa. Ph.D. dissertation. University of Port Elizabeth.

Robb, G.N., McDonald, R.A., Chamberlain, D.E., Reynolds, S.J., Harrison, T.J.E., Bearhop, S. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters 4: 220–223.

Robben Island Museum 2013. Integrated Conservation Management Plan 2013–2018. Draft Natural Environment Management Plan. Robben Island Museum, Cape Town.

Robinson, S., Chiaradia, A., Hindell, M. A. 2005. The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. Ibis 147: 483–489.

Robinson, J.A., Hamer, K.C., Chivers, L.S. 2002. Developmental plasticity in Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* in response to a period of extremely bad weather. Ibis 144: 344–346.

Ropert-Coudert, Y., Cannell, B., Kato, A. 2004. Temperature inside nest boxes of little penguins. Wildlife Society Bulletin 32: 177–182.

Rowlands, D.J., Frame, D.J., Ackerley, D., Aina, T., Booth, B.B.B., Christensen, C., Collins, M., Faull, N., Forest, C.E., Grandey, B.S., Gryspeerdt, E., Highwood, E.J., Ingram, W.J., Knight, S., Lopez, A., Massey, N., McNamara, F., Meinshausen, N., Piani, C., Rosier, S.M., Sanderson, B.M., Smith, L.A., Stone, D.A., Thurston, M., Yamazaki, K., Yamazaki, Y.H., Allen, M.R. 2012. Broad range of 2050 warming from an observationally constrained large climate model ensemble. Nature Geoscience 5: 256–260.

Roy, C., van der Lingen, C. D., Coetzee, J. C., Lutjeharms, J. R. E. 2007. Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. African Journal of Marine Science 29: 309–319.

Salton, M., Saraux, C., Dann, P., Chiaradia, A. 2015. Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. Royal Society Open Science 2: 140390, http://dx.doi.org/10.1098/rsos.140390.

Salzman, A.G. 1982. The selective importance of heat stress in gull nest location. Ecology 63: 742–751.

Saraux, C., Chiaradia, A., Le Maho, Y., Ropert-Coudert, Y. 2011. Everybody needs somebody: unequal parental effort in little penguins. Behavioural Ecology 22: 837–845.

Schamber, J.L., Esler, D., Flint, P.L. 2009. Evaluating the validity of using unverified indices of body condition. Journal of Avian Biology 40: 49–56.

Seddon. P.J. and Davis, L.S. 1989. Nest-site selection by Yellow-eyed penguins. Condor 91: 653–659.

Seddon, P.J. and van Heezik, Y. 1993. Behaviour of the jackass penguin chick. Ostrich 64: 8–12.

Seddon, P.J. and van Heezik, Y. 1991. Effects of hatching order, sibling asymmetries, and nest site on survival analysis of Jackass Penguin chicks. Auk 108: 548–555.

Sherley, R.B., Abadi, F., Ludynia, K., Barham, B.J., Clark, A.E, Altwegg, R. 2014. Age-specific survival and movement among major African Penguin *Spheniscus demersus* colonies. Ibis 156: 716–728.

Sherley, R.B., Underhill, L.G., Barham, B.J., Barham, P.J., Coetzee, J.C., Crawford, R.J.M., Dyer, B.M., Leshoro, T.M., Upfold, L. 2013. Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. Marine Ecology Progress Series 473: 291–301.

Sherley, R.B., Ludynia, K., Underhill, L.G., Jones, R., Kemper, J. 2012a. Storms and heat limit the nest success of Bank Cormorants: implications of future climate change for a surface-nesting seabird in southern Africa. Journal of Ornithology 153: 441–455.

Sherley, R.B., Barham, B.J., Barham, P.J., Leshoro, T.M., Underhill, L.G. 2012b. Artificial nests enhance the breeding productivity of African penguins (*Spheniscus demersus*) on Robben Island, South Africa. Emu 112: 97–106.

Sherley, R.B., Burghardt, T., Barham, P.J., Campbell, N., Cuthill, I.C. 2010. Spotting the difference: towards fully-automated population monitoring of African penguins *Spheniscus demersus*. Endangered Species Research 11: 101–111.

Sherley, R.B. 2010. Factors influencing the demography of endangered seabirds at Robben Island, South Africa: implications and approaches for management and conservation. PhD dissertation. University of Bristol, Bristol, UK.

Simmons, R.E., Barnard, P., Dean, W.R.J., Midgley, G.F., Thuiller, W., Hughes, G. 2004. Climate change and birds: perspectives and prospects from southern Africa. Ostrich 75: 295–308.

Stokes, D.L. and Boersma, P.D. 1998. Nest-site characteristics and reproductive success in Magellanic penguins (*Spheniscus magellanicus)*. Auk 115: 34–49.

Stokes, D.L. and Boersma, P.D. 1991. Effects of substrate on the distribution of Magellanic penguin (*Spheniscus magellanicus*) burrows. Auk 108: 923–933.

Suryan, R.M., Irons, D.B., Kaufman, M., Benson, J., Jodice, P. G.R., Roby, D.D., Brown, E.D. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. Marine Ecology Progress Series 236: 273–287.

Sutherland, D.R., Dann, P., Jessop, R.E. 2014. Evaluation of artificial nest sites for long-term conservation of a burrow-nesting seabird. Journal of Wildlife Management 78: 1415–1424.

Trathan, P.N., Fretwell, P.T., Stonehouse, B. 2011. First recorded loss of an emperor penguin colony in the recent period of Antarctic regional warming: implications for other colonies. PLoS ONE 6: e14738. doi:10.1371/journal.pone.0014738.

Tveraa, T., Sæther, B., Aanes, R., Erikstad, K.E. 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. Journal of Animal Ecology 67: 699–704

Varpe, Ø., Tveraa, T., Folstad, I. 2004. State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing. Oikos 106: 479–488.

Vleck, C.M. and Vleck, D. 2002. Physiological condition and reproductive consequences in Adélie penguins. Integrative and Comparative Biology 42: 76–83.

Walsberg, G. E. and Weathers, W. W. 1986. A simple technique for estimating operative environmental temperature. Journal of Thermal Biology 11: 67–72.

Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F., Ridoux, V. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. Ecology 78: 2051–2063.

Weimerskirch, H. 1992. Reproductive Effort in Long-Lived Birds: Age-Specific Patterns of Condition, Reproduction and Survival in the Wandering Albatross. Oikos 64: 464–473.

Weller, F., Cecchini, L.-A., Shannon, L., Sherley, R.B., Crawford, R.J.M., Altwegg, R., Scott, L., Stewart, T. and Jarre, A. 2014. A system dynamics approach to modelling multiple drivers of the African penguin population on Robben Island, South Africa. Ecological Modelling 277: 38–56.

Whittington, P., Klages, N., Crawford, R. J. M., Wolfaardt, A. C., Kemper, J. 2005. Age at first breeding of the African penguin. Ostrich 76: 14–20.

Williams, C.T., Kildaw, S.D., Buck, C.L. 2007. Sex-specific differences in body condition indices and seasonal mass loss in Tufted Puffins. Journal of Field Ornithology 78: 369–378.

Wilson, R.P. and Wilson, M-P.T. 1989. Substitute burrows for penguins on guano-free islands. Le Gerfaut 79: 125–131.

Wilson, R.P., Wilson, M-P. T., Duffy, D.C. 1988. Contemporary and historical patterns of African penguin *Spheniscus demersus*: Distribution at sea. Estuarine, Coastal and Shelf Science 26: 447–458.

Wolf, B.O. and Walsberg, G.E. 1996. Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. Journal of Experimental Biology 199: 451–457.

Wolfaardt, A. C., Williams, A. J., Underhill, L. G., Crawford, R. J. M., Whittington, P. A. 2009. Review of the rescue, rehabilitation and restoration of oiled seabirds in South Africa, especially African penguins *Spheniscus demersus* and Cape gannets *Morus capensis*, 1983−2005. African Journal of Marine Science 31: 31–54.

Wolfaardt, A. C., Underhill, L. G., Nel, D. C., Williams, A. J., Visagie, J. 2008. Breeding success of African penguins *Spheniscus demersus* at Dassen Island, especially after oiling following the Apollo Sea spill. African Journal of Marine Science 30: 565–580.

Yorio, P. and Boersma, P.D. 1994. Cause of nest desertion during incubation in the Magellanic Penguin (*Spheniscus magellanicus*). Condor 96: 1076–1083.

Young, B. 2012. Project with Bristol Zoo Gardens: Instrumented Nest Boxes for Grey Mouse Lemurs and African Penguins (NPSM17). Final BSc Project. University of Bristol, Bristol, UK.