

# **The endangered bank cormorant *Phalacrocorax neglectus*: the heat is on**

Understanding the effect of climate change and associated environmental variable changes on the breeding biology and population dynamics of the bank cormorant in the Western Cape, South Africa



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*For the birds*



## Abstract

The bank cormorant *Phalacrocorax neglectus* was listed as ‘Endangered’ in 2004, following a decrease of more than 60% in the total population from 1975–2011. It ranges from central Namibia to the Western Cape, South Africa, with most of the population occurring on offshore islands in Namibia.

The main reason for this study was to determine if climate change could be identified as a factor which has influenced the decreasing numbers of bank cormorants. This involved research on the heat stress behaviour, breeding success and population trends of the bank cormorant in the Western Cape, South Africa.

High environmental temperatures resulting in heat stress and storms with associated extreme environmental variables was predicted to cause breeding failures, decreasing breeding success. As a result, climate change can also affect long-term trends in the adult population of the bank cormorant, and this was examined using the population data of nine bank cormorant colonies in the Western Cape, South Africa.

A link existed between ambient and operative temperature, and the latter was used for statistical analysis. Mean operative temperatures of over 30°C were experienced. Temperatures were highest at the bank cormorant colony at Robben Island when three colonies were compared (Robben Island, Jutten Island and Stony Point). Increased environmental temperatures resulted in the average bank cormorant increasing its time spent employing thermoregulatory behaviour. Bank cormorants were shown to start gular fluttering at 21°C on average and spend all their time gular fluttering when they experienced an operative temperature of 34.2°C or higher. The birds also started employing this thermoregulatory behaviour at a lower temperature when on eggs or small chicks.

During the study period, the breeding success of the bank cormorant was not impacted by high temperatures at the three bank cormorant colonies studied. Wave and wind action, associated with storms, resulted in a lowered reproductive output during the breeding seasons of 2012 and 2013. Both incubation success and chick rearing success did not differ significantly between 2012 and 2013 for the three bank cormorant colonies at Robben Island, Jutten Island and Stony Point.

The study of long-term trends in colony sizes of nine bank cormorant colonies in the Western Cape, South Africa revealed a decrease in the bank cormorants breeding population. The decrease could not be directly associated with climate change in the region. An increase in the mean maximum temperatures and a decrease in the annual rainfall did not affect the bank cormorant numbers, but rather the fecundity. This resulted in a lagged effect of climate change on the bank cormorant population. Climate change and extreme weather events can cause massive breeding failures.





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# Chapter 1

## Introduction: an overview of the bank cormorant

### 1.1 Global climate change and seabirds

Global climate change due to anthropogenic impacts is now widely accepted (Clark 2008) and has been recognised as one of mankind's most dangerous threats to biodiversity (Simmons *et al.* 2004, Gregory *et al.* 2009), placing substantial stress on marine as well as terrestrial ecosystems (Grémillet and Boulinier 2009). The 2007 Climate Change Synthesis Report stated that the warming of the global atmosphere since the 1850s has been at a more rapid rate than at any other time in the past millennium (IPCC 2007). The temperature of the Earth's atmosphere is also predicted to become warmer in the next few decades than at any time in the past 40 million years (IPCC 2007).

The Intergovernmental Panel on Climate Change (IPCC) stated that global average surface temperatures have already increased as a result of anthropogenic production of greenhouse gases, especially carbon dioxide (CO<sub>2</sub>) (IPCC 2007). Greenhouse gases trap solar energy within the Earth's atmosphere and their increase has resulted in the Earth's mean temperature warming. Warming has increased with more than 0.6°C in the last century with at least c. 0.2°C per decade in the 30 years before the early 2000s (Simmons *et al.* 2004, Hansen *et al.* 2006), with considerable acceleration in the past 50 years leading up to 2009 (Grémillet and Boulinier 2009). Other impacts of global climate change and global warming include a rising sea level because of thermal expansion and melting ice caps, changes in precipitation patterns, increased variability in global climate and increased intensity and frequency of extreme weather events (Clark 2008, Boersma and Rebstock 2014). The frequency of such extreme warm and precipitation events have increased dramatically in the past half a century after the 1960s (IPCC 2013).

The rise in temperature has created concerns for the biological and ecological processes that affect species' ranges and distributions; phenology and physiology of species; cycles, composition and interactions of communities; and the structure and dynamics of ecosystems (Croxall *et al.* 2002). Recent monitoring of certain key environmental parameters in South Africa confirms the occurrence of environmental changes; these physical changes in the atmosphere and ocean are predicted to have important consequences for marine ecosystems (Clark 2008). Understanding how these ecosystems respond to current climate change is important in helping predict their response to future climate change (Bolger *et al.* 2005).

Various reviews on the potential effects of global warming and climate change on biodiversity have identified Africa as the most vulnerable of the continents (IPCC 2001, Simmons *et al.* 2004). During the 1990s it became apparent that long-term climate change might influence some seabird species in

the Southern Ocean (Crawford and Cooper 2003, Weimerskirch *et al.* 2003). The impacts of climate change on animals or birds can be divided into indirect impacts (i.e. influencing food resources) or direct physiological effects, such as thermoregulation (Oswald and Arnold 2012). Most studies on the effects of climatic change on species populations have focused on the indirect consequences – habitat availability and quality, changes in biological processes and food resource availability and quality – as drivers of species' distribution, population changes and behavioural changes (Oswald and Arnold 2012).

Studies have determined that South Africa is undergoing general warming (Kruger and Sekele 2013), and to understand the potential effects of climate change on African birds, we need first to understand the predicted effects of climate change in Africa. The IPCC have predicted five major effects (IPCC 2001): 1) increased mean seasonal temperatures, 2) decreased rainfall in most areas, 3) increased frequency of El Niño Southern Oscillation effects in southern Africa, 4) increased frequency of severe weather anomalies and 5) increased frequency of fires due to higher temperatures and decreased rainfall. Of these, the dominant consequence is increased air temperature at the ocean and land surface (Oswald and Arnold 2012). Increased temperatures influence biotic responses (processes) across various taxa, which include phenology, demography, distribution and individual behaviour (Oswald and Arnold 2012). However, predictions of the impacts of global warming on endotherms (especially mammals and birds) have generally been assumed to occur through ecosystem changes, rather than direct heat stress (Gaston *et al.* 2009).

Anthropogenic activities and resulting environmental changes affect all components of marine food webs, including seabirds that act as top predators in the marine food chain (Grémillet and Boulinier 2009). Various threats, including climate change, overfishing and other modifications to marine ecosystems may cause seabird populations to either modify their foraging ecology and therefore still survive and reproduce in the same distribution, change their range and distribution or eventually go extinct (Grémillet and Boulinier 2009, Lewison *et al.* 2012).

Oswald and Arnold (2012) indicated that seabirds can be used as bio-indicators for changes in the climatic environment and because seabirds are top marine predators and climate change that alters the marine ecosystem at lower levels will also influence seabird populations (Crawford and Altwegg 2009). The influence of climate change on seabirds has been especially noticeable at high latitudes (Crawford and Altwegg 2009) and available evidence suggests that predicted climatic warming might raise environmental temperatures beyond that tolerable to seabirds (Oswald and Arnold 2012). Kruger and Sekele (2013) have indicated increasing trends in maximum daily temperature in South Africa, especially in the western half of the country.

Therefore, climate change has the potential to affect species fitness severely (Boyles *et al.* 2011). The IPCC Fifth Assessment Report (IPCC 2013) stated that each of the past three decades leading up to

the 2010s, have been warmer than any other decade in recorded history, with the first decade of the 21<sup>st</sup> century being the warmest. Southern hemisphere seabirds are amongst the most threatened bird groups, with their populations continuously declining (Boersma and Redstock 2014). The purpose of this study is to determine the direct impact of high temperatures and other extreme weather events on the breeding success and behaviour of breeding bank cormorants *Phalacrocorax neglectus*. The study also establishes the long-term effects of climate change on the species' population trends as on-going environmental change and anthropogenic impacts, possibly linked to global climate change will have long-term effects and often-catastrophic effects on seabird populations (Lewison *et al.* 2012).

## **1.2 High temperatures, heat stress and storms**

The capacity of a seabird to cope with a change in its thermoregulatory needs will depend on its morphology, physiology and behaviour (Oswald and Arnold 2012). Adult seabirds cope with extreme weather events far better than eggs or chicks. Eggs and chicks can be lost during storms, rains or wind linked to extreme weather conditions (Mallory *et al.* 2009a). Breeding adult seabirds also respond with active evaporative cooling to heat stress caused by high temperatures. This can lead to adults abandoning nests to avoid dehydration from the evaporative cooling (Gaston *et al.* 2002).

Rapidly changing environmental temperatures might change the selective pressures acting on all animals, because temperature is one of the most important factors impacting energy and water balance. Rising environmental and atmospheric temperatures as a result of climate change may challenge the thermoregulatory abilities of both ectotherms and endotherms (Boyles *et al.* 2011). The ability of endotherms to maintain body temperature different to that of the environment is facilitated by heat produced through metabolic processes, an insulation layer, and thermoregulatory behaviour that initiates heat loss or heat production in response to environmental temperature change (Wilson and Grémillet 1996, Boyles *et al.* 2011); this is especially true if the temperatures exceed a species' thermal limits (Oswald and Arnold 2012). Although endotherms are more capable of maintaining internal thermal homeostasis under extreme environmental conditions than ectotherms, there are also limits to their capacity to cope with variations in the thermal environment (Oswald and Arnold 2012).

There are examples of seabird breeding failure and mortality in response to extreme weather events in the South Atlantic Ocean, for example, Boersma and Redstock (2014) found that intense storms could increase adult mortality and cause a decline in reproductive success in seabirds. Storms and extreme heat waves affect Magellanic penguins *Spheniscus magellanicus*, breeding at Punta Tombo, South America (Boersma and Redstock 2014). High environmental temperatures have also been found to cause breeding failures in Brünnich's guillemots that breed in the Arctic (Gaston *et al.* 2002). Therefore, I hypothesised that climate change, through increasing atmospheric temperatures and the increased frequency of severe weather events during the breeding season, have influenced the long-



term population size and demography of the endangered bank cormorant, by negatively affecting adult mortality and its reproductive success.

Since the mid-1900s, many studies have been conducted on the thermoregulatory mechanisms of seabirds (Oswald and Arnold 2012). Seabirds regularly encounter ambient environmental temperatures that exceed their upper critical temperature limit (Oswald and Arnold 2012) and high temperatures can have direct effects on the survival and reproduction of some seabird species (Gaston *et al.* 2009).

Breeding utilizes a substantial portion of an adult bird's time and energy budget (Oswald and Arnold 2012). In many cases the energy and/or time that is supposed to be invested in reproduction and care of their young, might have to be used for active thermoregulation and heat stress behaviour or the individual bird could risk death from hyperthermia (Oswald and Arnold 2012). Heat stress because of high temperatures has been recorded as an important element in the breeding ecology of many seabirds (Gaston *et al.* 2009), potentially leading to a decreased reproductive rate (Oswald and Arnold 2012).

Heat stress can cause breeding failures during unusually warm breeding events (Gaston *et al.* 2002, Mallory *et al.* 2009a). The risk of breeding failure is increased when seabirds, such as the bank cormorant, have thermally exposed breeding sites and thus have little opportunity to avoid direct solar radiation (Oswald and Arnold 2012). Open nest sites leaves them exposed to the elements and extreme environmental heat gain (Oswald and Arnold 2012), and therefore, many cormorant species are subject to overheating at the nest (Lasiewski and Snyder 1969). Overheating is further aggravated by their dark plumage (Lasiewski and Snyder 1969). I predicted that the bank cormorant increases its thermoregulatory activity during periods of high heat loads. Breeding attempts might also be abandoned if extreme ambient temperatures challenge the ability of adults to maintain suitable incubating and brooding schedules during the breeding season (Oswald and Arnold 2012).

Behavioural modifications can reduce thermal stress, such as postural adjustments to minimize dark plumage exposure to the sun; evaporative heat loss through gular fluttering and panting; and ptilomotion, the raising of scapular feathers, or wing drooping to increase convective heat loss (Oswald and Arnold 2012). Gular fluttering causes evaporative cooling of the bird due to the movement of air through the respiratory tract (Bartholomew *et al.* 1968). Under severe heat loads, birds utilize all these behaviours (Bartholomew and Dawson 1979). Older nestling and adult cormorants compensate for the excessive heat load through these behavioural adjustments and gular fluttering, which has a low energy cost, but a high rate of water loss (Lasiewski and Snyder 1969).

Orientation towards the sun may not be very effective in the case of the bank cormorant, because the entire plumage is dark, increasing the heat load from solar radiation (Oswald and Arnold 2012).

Postural adjustments, such as wing drooping, can however be effective as they are related to wind direction; for example, certain gull species react with postural adjustments that conform to meteorological conditions (Bartholomew and Dawson 1979). Postural adjustment is also important when shielding chicks from the sun, and this postural brooding behaviour of Suliformes is important for the survival of the young (Lasiewski and Snyder 1969). However, the possible suite of postural adjustments may be limited during incubation (Oswald and Arnold 2012), when movement is limited.

The most effective way to lose excess heat is through evaporative heat loss mechanisms; however this can lead to osmotic stress if birds cannot not leave the nest during long incubation or brooding shifts (Oswald and Arnold 2012) when they need to protect their eggs and chicks from the physical environment and predators (Bartholomew and Dawson 1979). Certain cormorant species elevate their body temperature during high heat loads to reduce water loss during hyperthermia (Lasiewski and Snyder 1969). This is a general avian response to heat stress (Lasiewski and Snyder 1969). I therefore predicted that the bank cormorant will increase their thermoregulatory behaviour to cool down during times of high heat loads so as to avoid risking their own survival.

The study species, the bank cormorant, is classified 'Endangered' and is endemic to the Benguela upwelling system off south-western Africa (Crawford *et al.* 2008a, BirdLife International 2013). The species was listed as 'Endangered' in 2004 following a decline in the general population from c. 9 000 breeding pairs between 1975 and 1981 (Cooper 1981) to approximately 5 000 breeding pairs in 1995 to 1997 (Crawford *et al.* 1999), a maximum of 3 600 breeding pairs in 2007 (Crawford *et al.* 2008a, Sherley *et al.* 2012), and c. 3 000 breeding pairs in 2011 (Crawford *et al.* 2012). This presents a decline of 46% in 17 years ending in 2002 and a decrease of 66% in the 40 years leading up to 2011 (over three generations) (du Toit *et al.* 2002).

The bank cormorants' current breeding distribution ranges from Swakopmund (22° 68' S, 14.53° E), central Namibia to Quoin Rock (34°46' S, 19°40' E) (the most eastern colony), Western Cape, South Africa (du Toit *et al.* 2002). This is similar to its breeding distribution during the 1980s (Cooper 1981). The non-breeding range of the bank cormorant ranges from Hoanibimond, northern Namibia (19°27' S; 12°43' E), to Die Walle, Western Cape, South Africa (34°46' S; 19°54' E) (du Toit *et al.* 2002). This distribution roughly reflects that of beds of kelp bamboo *Ecklonia maxima* (Crawford *et al.* 2008a). The coast length of the bank cormorant's range is c. 1 500 km (Cooper 1981).

### **1.3 The Benguela upwelling system**

The cool, eastern boundary Benguela Current and associated upwelling system stretches along the west coast of southern African (Abrams and Griffiths 1981, Shelton *et al.* 1985) and is one of the four major upwelling regions of the world (Shannon and Jarre-Teichman 1999). It can be sub-divided into the northern and southern systems that split at the upwelling cell at Lüderitz, Namibia

(Ludynia 2007). Water rises from an approximate depth of between 100 m and 300 m. The upwelling process draws cold, nutrient-rich bottom water into the photic zone, fuelling primary production in the ocean (Arntz *et al.* 2004). Coastal upwelling along the west coast of southern Africa happens seasonally, mainly from October to April, with a peak in intensity during the first four months of the year (Roy *et al.* 2001).

The Benguela upwelling system maintains an average water temperature of 13.4°C while air temperatures over coastal areas may reach over 35°C (Wilson and Grémillet *et al.* 1996). However, temperature, salinity and productivity in the water mass fluctuate seasonally with upwelling (Cury and Shannon 2004) and the average air temperature ranges between 10–27°C (Abrams and Griffiths 1981).

The coastal waters of the Benguela region are characterized by kelp beds (mostly *Ecklonia maxima* and *Laminaria pallida*) which dominate where the cold Benguela water exerts influence through upwelling (Velimirov *et al.* 1977). The system is highly productive and historically supported abundant populations of pelagic fish (Crawford 2007) and seabirds. Seabird communities are most diverse during the austral winter when migratory species arrive in their non-breeding period (Abrams and Griffiths 1981, Adams *et al.* 1992). Water temperature, distance from shore, salinity, depth and air temperature affect the seabird distribution to a lesser extent than the upwelling along the coastal region (Abrams and Griffiths 1981).

Marine and coastal ecosystems are under constant threat of degradation and disruption by human activities (David *et al.* 2003). Bank cormorants are sensitive to disturbance (Cooper 1981). The human disturbance at breeding sites has been one of the main factors restricting the distribution of seabird breeding colonies along the southern African coast (Bartlett *et al.* 2003). Bank cormorants are especially sensitive to human disturbance during their breeding season (Crawford *et al.* 2008a). Human interference at breeding sites can cause adults to abandon their nests, leaving eggs and small chicks vulnerable to kelp gull *Larus dominicanus* predation (Cooper 1981).

However, the Benguela upwelling system is currently undergoing various changes, affecting the marine environment, due to over-fishing and climate change (Braby *et al.* 2012). Global warming is affecting upwelling activities in the system, resulting in a gradual increase in Sea Surface Temperature (SST) (Cury and Shannon 2004) and reduced upwelling intensity (Ludynia 2007). Research is beginning to identify seabird relationships with physical habitat features and the environment (Ribic and Ainley 1997).

Fifteen seabird species, including the bank cormorant, breed in the Benguela upwelling system, of which seven of these are endemic to southern Africa (Kemper *et al.* 2007). This abundance of seabirds results from enhanced productivity associated with nutrient upwelling in this region during

the spring and summer, increasing primary production and therefore prey availability during the winter (Abrams and Griffiths 1981, Adams *et al.* 1992). Local bird assemblages can usually be found in these areas of upwelling and mixing (Hunt and Schneider 1987).

#### **1.4 The bank cormorant**

Cormorants belong to the family Phalacrocoracidae in the order Suliformes. Cormorants' general form and shape resemble that of divers and their feathers are less water repellent than those of most other water birds (Grémillet *et al.* 2005). This partial wettability of their feathers may limit their seaward dispersal (Hunt and Schneider 1987). Cormorants are long-lived birds and their life expectancy is about five to seven years, but some live to be more than 15 years old (Kemper *et al.* 2007). In southern Africa, five cormorant species occur: the Cape cormorant *P. capensis*, white-breasted cormorant *P. carbo lucidus*, reed cormorant *P. africanus*, crowned cormorant *P. coronatus* and bank cormorant.

Male and female bank cormorants are similar in appearance, but the male is notably larger (Cooper 1985a). This heavily built bird's weight ranges from approximately 1700–2100 g – little has been published about the other measurements of the bank cormorant (Cooper 1985a). Adults appear entirely black, but in sunlight the wings, upper mantle and scapular have a glossy, brown-bronze appearance. During the pre-breeding period, they also display white filoplumes on the side of their head and neck and a white patch on their rump, which is lost during the incubation period because of constant preening of the feathers (Cooper 1985a). The iris of the adult's eye divides into two colours: orange-brown above the pupil and blue-green below (Cooper 1985a).

During a 10-year period from 1971–1980, 44 breeding colonies were found to occur with c. 9 000 breeding pairs (Cooper 1981). Most colonies consisted of between 20–100 nests (Cooper 1986), with the exception of two large Namibian colonies at Ichaboe and Mercury Islands. By 2002, 52 breeding localities had been described between Hollamsbird Island, Namibia, and Quoin Rock (du Toit *et al.* 2002). Currently, the two colonies on Mercury and Ichaboe Islands, in the southern Namibian part of the bank cormorant's range, support between 70–80% of the breeding population, while smaller colonies in South Africa and Namibia support the remainder (Ludynia *et al.* 2010).

The most drastic decrease in the bank cormorant's population occurred in Namibia with 7 166 pairs in 1978–1980 compared to c. 2 500 breeding pairs in 2007 (Crawford *et al.* 2008a). Bank cormorants breeding at Mercury Island experienced a large decrease in the 1980s and 1990s. During the 1970s, Mercury Island supported c. 46% of the total bank cormorant population and approximately 71% of the total population occurred in Namibia on Ichaboe and Mercury Islands (Cooper 1981, Crawford *et al.* 1999). In 2006, Mercury Island supported about 55% of the total bank cormorant breeding population (Sherley *et al.* 2012). Crawford *et al.* (1999) stated that the decreases from 1995–1997 at

various Namibian colonies did not occur at the same time; this suggests that different factors might have influenced the overall decline in the number of bank cormorants. The remarkable decline in the overall bank cormorant population provided the motivation for this research.

In South Africa, bank cormorants breed during the austral winter, whereas in Namibia they breed during summer (Sherley *et al.* 2012). Colonies are mostly restricted to islands and offshore rocks, but where this species has colonized mainland breeding locations, they are usually on rocky cliffs, inshore rocks or high boulders and inaccessible from terrestrial predators (du Toit *et al.* 2002). They also breed on man-made (artificial) structures such as breakwaters ('dolosse') or old jetties (du Toit *et al.* 2002, Bartlett *et al.* 2003). These sites can be in the sea or near to the water's edge (Cooper 1986). Kelp beds usually occur adjacent to breeding sites (Cooper 1985b). This species is sensitive to disturbance, particularly during the breeding season and when humans come too close to a breeding colony, adults frequently move away from their nests, leaving the eggs and/or chicks exposed to predation by kelp gulls (Cooper 1981).

Bank cormorants construct large, heavy nests, engineered mainly from seaweed. The nesting material is gathered during short trips in the day by diving in inshore shallow kelp beds, but material can also be stolen from other nests in the absence of nest owners (Cooper 1986). Cooper (1986) found after examining two nests that less than 4% of a nest consisted of other materials, including feathers, sticks and artificial material. Building and working on the nest continues throughout the breeding season (Cooper 1986). Nest construction starts when a male bank cormorant places nesting material at a suitable nest site (Cooper 1986). Nesting material is collected almost exclusively by male birds prior to incubation (Cooper 1986).

A bank cormorant reaches sexual maturity at three years of age (Cooper 1985a) and adult and non-adult birds do not occur in the same foraging areas (Cooper 1985b). The species seldom moves beyond its foraging range, as determined by the kelp beds (Cooper 1985b). They lay a mean of 2.02 eggs per clutch, with three eggs being the largest recorded clutch size (Cooper 1987). Both the male and female share incubation duties equally (Cooper 1987). The eggs are incubated on the bare, webbed feet. This may be to isolate the eggs from the damp nest and to warm the eggs on the heavily vascularized feet (Cooper 1987). Eggs are incubated for a period of roughly 30 days (Cooper 1986) and chicks are reared for approximately 55 days (Cooper 1978). Bank cormorants are primarily sedentary, with some post-breeding dispersal of fledglings (du Toit *et al.* 2003).

## **1.5 Thesis outline**

This thesis identifies the impact of climate change and associated temperature increases and storm events on the population and breeding biology of the endangered bank cormorant. It includes three chapters describing the research done over a two-year study period, including the heat stress

behaviour during the breeding period, breeding success of the bank cormorant and long-term population decline associated with long-term climate change.

Breeding bank cormorants were observed to determine their thermoregulatory behaviour at the nest during incubation and chick rearing. The breeding success of the cormorant was related to a number of environmental variables to determine which variables affect the incubation success and the chick rearing success of the species, resulting in a decrease in their breeding success. Climate change was also tested against the decrease of the bank cormorant population, to determine if climate change has an impact on bank cormorant breeding numbers.



## Chapter 2

### The influence of environmental temperatures on the thermoregulatory behaviour of the breeding bank cormorants *Phalacrocorax neglectus*

#### 2.1 Introduction

Temperature is a vital factor in affecting the water balance and energy of terrestrial animals; therefore, changing environmental temperatures may influence fitness (Boyles *et al.* 2011) and have direct effects on the survival of some seabird species (Gaston *et al.* 2001). Rising environmental and atmospheric temperatures may challenge the thermoregulatory abilities of birds. Thermal stress is a key element in the breeding ecology of many seabirds (Gaston *et al.* 2001), thus the implementation of a thermal defence strategy by breeding adult seabirds is of great importance (Salzman 1982).

The bank cormorant *Phalacrocorax neglectus*, an endemic seabird occurring off the west coast of southern Africa (Cooper 1981), is an endothermic species. Endotherms maintain their body temperature in a narrow range, mainly through metabolic processes in response to environmental temperature fluctuations (Boyles *et al.* 2011). High environmental temperatures may lead to the employment of behavioural and physiological adjustments by birds to prevent overheating (Downs and Ward 1997). These adjustments include: postural adjustments to minimize exposure to the sun; evaporative heat loss through gular fluttering and panting; raising of scapular feathers and wing drooping to increase convective heat loss (Bartholomew *et al.* 1968, Oswald and Arnold 2012). When environmental temperatures exceed a species' thermal limits, adult cormorants must compensate for excessive heat gain through these adjustments (Lasiewski and Snyder 1969, Downs and Ward 1997, Boyles *et al.* 2011). Under severe heat loads, birds may utilize all these behaviours (Bartholomew and Dawson 1979).

Many open-nesting seabirds are threatened by high environmental temperatures (Salzman 1982), because this leaves them exposed to the elements and extreme environmental heat gain (Oswald and Arnold 2012). Adult nesting bank cormorants are often subject to overheating at their exposed nests sites (Cooper 1986), further aggravated by their dark plumage (Lasiewski and Snyder 1969). Breeding adults, incubating eggs or brooding small chicks, have little flexibility when responding to environmental fluctuations (Durant 2004).

However, certain behavioural modifications are more effective than others are. Orientation towards the sun may not be very effective in the case of the bank cormorant as the entire plumage is dark, increasing the heat load from solar radiation (Oswald and Arnold 2012). Posture adaptations can however be effective as they may be related, like wing drooping, to wind direction and speed. Other seabird species, such as the masked booby *Sula dactylatra*, have been found to droop their



wings to facilitate air circulation and thus increase passive heat loss at ambient temperatures below body temperatures (Bartholomew 1966). However, postural adjustments can be limited during the incubation period (Oswald and Arnold 2012). Postural adjustment is also important when shielding chicks from the sun, and this brooding behaviour of Suliformes is important for the survival of the young (Lasiewski and Snyder 1969).

The most effective way for birds to get rid of excess heat is through evaporative heat loss mechanisms; in the case of cormorants this is achieved through gular fluttering. However this can lead to osmotic stress because some adults do not leave the nest when incubation or brooding period (Oswald and Arnold 2012), due to the need to protect their eggs and chicks from potential predators and the physical environment (Bartholomew and Dawson 1979). Like many other birds, some cormorants elevate their body temperature slightly when experiencing high heat loads to conserve energy and reduce water loss (Lasiewski and Snyder 1969).

The breeding period utilizes a substantial portion of an adult bird's energy and time budget (Oswald and Arnold 2012). Increasing energy expenditure on active thermoregulation decreases the time and energy available for reproduction and care of their young; alternatively the bird risks death from hyperthermia (Oswald and Arnold 2012). Potentially, the effect of high temperatures on breeding activity leads to a decreased reproduction rate (Oswald and Arnold 2012), because heat stress can cause breeding failures (Gaston *et al.* 2002) during unusually warm breeding events (Mallory *et al.* 2009a).

The goal of this chapter was to determine the relationship between environmental temperature and the nesting behaviour of the bank cormorant using operative temperature as a measurement. Operative temperature, rather than ambient temperature, was expected to better fit models of thermoregulation, as they reflect the temperature an animal experiences (Bakken *et al.* 1985). It was expected that thermoregulatory behaviour would increase with higher environmental temperatures, risking the survival of the breeding adult (Durant *et al.* 2004). It was also expected that gular fluttering would be the main method of cooling for the bank cormorant, as seen in previous studies (e.g. Bartholomew 1966, Bartholomew *et al.* 1968).

## **2.2 Materials and Methods**

### **2.2.1 Study sites**

The study was undertaken at three bank cormorant colonies in the Benguela upwelling system: Stony Point (34°22' S, 18°53' E), Robben Island (33°48' S, 18 22' °E) and Jutten Island (33°04' S, 17°57' E), in the Western Cape, South Africa (Figure 2.1). Robben Island is situated 13 km north of Cape Town, in Table Bay. The Stony Point colony is located at Betty's Bay and Jutten Island is in the mouth of Saldanha Bay. At Stony Point and Jutten Island the bank cormorants nest on large, naturally

occurring rocks near the water's edge, whereas at Robben Island the birds breed on the man-made 'dollos' structures, comprising the island's harbour wall (Figures 2.2, 2.3 and 2.4).

### 2.2.2 Temperature data collection

Operative temperature ( $T_e$ ) measurements can be used to determine the thermal environment of the studied animal as it is related to the temperature of the environment (Bakken *et al.* 1985).  $T_e$  can be measured with the help of a suitable model or taxidermic mount with low heat capacitance (Bakken *et al.* 1985) that mimics the thermal properties of the studied species. The  $T_e$  can be described as the equilibrium temperature an organism would reach in the absence of metabolic heat production or evaporative water loss (Downs and Wards 1997)

In this study, hollow copper spheres, spray-painted matt-black were used to measure  $T_e$ . These had the same diameter as a bank cormorant's body (115 mm), determined by measuring the chest circumference of a dead bank cormorant specimen. These mounts, rather than taxidermic mounts, were used as they provide a suitable model for measuring  $T_e$  (Bakken *et al.* 1985, Walsberg and Wolf 1996), are generally more durable in harsh environmental conditions (Bakken 1992) than taxidermic mounts, and are easier to construct and use, especially given the endangered status of the bank cormorant which prevents collection of skins for taxidermic mounts. Using a hollow copper body can result in faster time responses to changes in thermal conditions (Bakken 1992). The walls of each sphere were 0.9 mm thick and each sphere was 11.5 cm in diameter. Copper was used as it has high thermal conductivity (Downs and Ward 1997). Maxim ibuttons™ (accurate to 0.0625°C for a range of -40 to 85°C) were placed in the spheres to measure  $T_e$ , without touching the sides of the sphere. Two ibuttons (in custom-made ibutton readers) were placed in each sphere for redundancy. Each sphere consisted of two hemispheres which were attached with glue and Tesa Tape and bolted together. These spheres were then mounted 10–20 cm above the ground to replicate the position of a bird on its nest. Mounts were attached to metal rods that were in turn attached to the end of a cement brick and insulating rubber was used to prevent the different metals from the sphere and rod touching and oxidising (Figure 2.5).

Ambient temperature ( $T_a$ ) was also measured.  $T_a$  can be defined as the temperature of the air in shaded and sheltered conditions and this is used to describe the environmental temperatures of the studied bank cormorant. For the  $T_a$  measurements, two ibuttons were placed into a white Stevenson's radiation screen (Figure 2.5). These screens were similarly placed onto metal bars (5 x 3.5 x 40 mm) and attached to the same cement brick on the other end. This entire setup was then placed near to each colony, without disturbing the nesting birds, to ensure that recorded conditions were similar to those experienced by nesting birds.

All iButtons were programmed to take temperature readings at 10 minute intervals for the duration of fieldwork. ColdChain Thermodynamics software was used for programming and the extraction of the data. Data were extracted every one to three weeks and the iButtons were also re-programmed at this interval. Data were stored as CSV files.

### 2.2.3 Behavioural data collection

Data for behavioural analysis were collected with the help of filming equipment during both the 2012 and 2013 breeding seasons (Figure 2.6). Using digital recorders result in minimum disturbance of the site and can produce good quality images (Pierce and Pobprasert 2007). Behavioural responses were studied while keeping a record of the microclimate. Two to four Sony video cameras were mounted on tripods approximately 30 m from the nearest nest in each colony. During the 2012 breeding season all data were recorded using the cameras and a Digital Video Recorder (DVR). The system was upgraded in 2013 to store data directly onto 32 GB memory cards. Data were then transferred onto an external hard drive. The video cameras were placed in CCTV camera housings to protect them from weather, water and bird damage. The cameras were focussed on the nests with the help of an external LCD screen that connected directly to the camera.

The Robben Island system was run through the island's main 220 V AC electricity supply. Due to a lack of electricity source at the Stony Point and Jutten Island colonies, portable systems were used. These consisted of two car batteries and an inverter to convert the 12V DC from the batteries to the 220V AC needed to run the DVR and the cameras. The batteries were recharged overnight using a generator.

During the 2012 fieldwork season, cameras only focused on one nest and only full days were filmed (07h00 to 18h00). During analysis of the videos, it was found that the videos could be analysed with two to three nests in one shot. This ensured that more data could be collected during one day's filming during 2013. In addition, the filming protocol was modified to only a few hours a day, as high temperatures (e.g. during midday) were needed for thermoregulatory behaviour to take place, and the light quality in the morning and afternoon was too bad to allow behavioural analysis.

Videos were watched to analyse heat stress behaviour of the nesting birds. A list of all possible nesting behaviours was made (Table 2.1). A software package, JWatcher v. 0.9 (Blumstein *et al.* 2000) was used for the quantitative analysis of behaviour, and the behaviours were programmed with key codes onto this programme. JWatcher was then used to record the nesting bird's behaviours in real time, while videos were watched (Figure 2.7). Mutually exclusive behaviours were programmed to stop when another started (i.e. gular fluttering had to stop when the beak was closed).

To determine the relationship between temperatures and nesting heat stress behaviour from the 2012 and 2013 data, 30 randomly selected hours was watched for each year, resulting in 360 observed 10-minute periods. Only hours between 09h00 and 17h00 were selected, as light quality on the videos was poor before and after those times. If the lighting quality was too poor for behavioural analysis in a randomly selected hour, another hour was selected randomly to replace it. During the 60 h of observations, eggs and chicks were never left alone by an adult.

Each hour was divided in to six 10-minute periods and analysed separately. When the film started, JWatcher was set to start and behaviour recordings started with a key press. As the programme and the video could not be started at exactly the same time, the starting time of the video and the starting time of a behaviour was manually adjusted and edited before data were saved. The JWatcher data capture session was set to automatically end after 10 minutes. This activity was repeated for the six 10-minute sessions to ensure data capture for the entire hour.

The observations and recordings of behavioural and temperature data allowed me to describe the various types of thermoregulatory behaviour associated with the nesting behaviour of bank cormorants and to correlate specific patterns of behaviour with environmental and operative temperatures as experienced by the birds at a colony.

#### 2.2.4 Statistical analysis

The Underhill-Zucchini Moulting Model (Underhill and Zucchini 1988) was used to describe the relationship between thermoregulatory behaviour and operative temperature. This model was originally designed to estimate the parameters involved with the timing of primary moult in birds. In summary, birds are observed in three categories and each bird has a date associated with the record: birds with old primary feathers which have not yet started moult and will do so at some unknown time in the future; birds in moult, when the extent of primary feather replacement can be measured; and birds which have completed moult, and have done so at some unknown point time in the past. The Underhill-Zucchini Moulting Model uses data from the categories to estimate three parameters: the mean date of start of moult, the duration of moult and the standard deviation of the start date. It involves the assumption that the start dates of moult have a normal distribution with the mean and standard deviation described above. This includes the start time and the duration as parameters and a measure of variation within a population. The date of completion of moult is estimated as the date of start of moult plus the duration. The model parameters are estimated by the method of maximum likelihood. Erni *et al.* (2013) developed software for the implementation of this moult model in R (R Development Core Team 2009). This particular implementation incorporates the flexibility to model the three parameters as linear functions of explanatory variables, and to undertake model selection in a standard statistical framework. Prior to the Underhill-Zucchini Moulting Model, linear regression had been used to estimate the parameters of moult, but this was incorrect because it violated the

underlying assumptions of linear regression; details of this are discussed by Underhill and Zucchini (1988).

This model can be used in the context of estimating the parameters of gular fluttering. I observed birds in three analogous categories: birds at low temperatures which had not yet started gular fluttering and would do so when some unknown, but higher, threshold temperature for that bird was reached; birds which were gular fluttering, and in which the extent of gular fluttering could be measured, and for which the temperature could be measured; and birds which were gular fluttering continuously, and had done so since some unknown, but lower, threshold temperature for that bird had been reached. Thus the Underhill-Zucchini Moulting Model is appropriate for estimating the parameters of gular fluttering: the average temperature at which gular fluttering commences (the threshold temperature), the temperature range in which gular fluttering goes from 0% to 100%, and the standard deviation of the threshold temperature in the population. The moulting model can be used with data which is censored or simplified in various ways (Underhill and Zucchini 1988); in this case the model with Data Type 2 was appropriate because all the birds were available for observation at all temperatures. Underpinning the model is the assumption that the distribution of mean starting dates for the birds in the population has a normal distribution, and the mean and standard deviation of this normal distribution are parameters which are estimated.

I exploited the flexibility of the Erni *et al.* (2013) implementation to include explanatory variables into the model. I investigated whether there were differences between the three colonies and the breeding state of the bird at the nest. Breeding state was categorised into three levels: Incubation (adult sits on eggs), small to medium woollies (adult sits on chicks) and large woollies (chicks can thermoregulate and the adult stands next to nest). Model selection was based on the Akaike Information Criterion (AIC).

## 2.3 Results

### 2.3.1 Ambient and operative temperatures

Operative temperatures were higher than ambient temperatures during the day ( $t_{358} = 16.98$ ,  $p < 0.001$ ). The two measures were strongly correlated ( $r_{355} = 0.67$ ,  $p < 0.05$ ) (Figures 2.8 and 2.9).

Ambient temperatures during the analysed hours reached a maximum of 29.9°C, whereas operative temperatures regularly exceeded 35°C, with a maximum of 39.7 °C (Figure 2.5). The largest difference between  $T_a$  and  $T_e$  was 12.8°C (at  $T_e$  29.4 and  $T_a$  16.7°C). The hourly mean temperatures indicate that the warmest part of the day for  $T_e$  was at noon (30.4°C) and for  $T_a$  at 13h00 (19.0°C) (Figure 2.9).

Robben Island's operative and ambient temperature were significantly higher than those of Stony Point ( $T_a$ :  $t = -3.9$ ,  $p < 0.001$ ,  $T_e$ :  $t = -6.5$ ,  $p < 0.001$ ) and Jutten Island ( $T_a$ :  $t = -5.1$ ,  $p < 0.01$ ,  $T_e$ :  $t = -5$ ,  $p < 0.001$ ), but there was no significant difference between temperatures at Stony Point and Jutten Island ( $T_a$ :  $t = 1.2$ ,  $p > 0.1$ ,  $T_e$ :  $t = -1.4$ ,  $p > 0.05$ ). For all three colonies, the average difference between  $T_e$  and  $T_a$  was 5–6 °C (Figure 2.10).

### 2.3.2 Correlated behaviours

Certain thermoregulatory behaviours of bank cormorants were positively correlated ( $r > 0.2$ ) (Table 2.2). Strong positive relationships existed between gular fluttering and head up ( $r_{364} = 0.66$ ,  $p < 0.01$ ); and head down and beak closed ( $r_{363} = 0.55$ ,  $p < 0.01$ ). Weaker positive correlations existed between wings propped and crouching ( $r_{362} = 0.25$ ,  $p < 0.01$ ); beak closed and standing ( $r_{364} = 0.23$ ,  $p < 0.01$ ); wings closed and standing ( $r_{364} = 0.26$ ,  $p < 0.01$ ); wings propped and gular fluttering ( $r_{362} = 0.23$ ,  $p < 0.01$ ); and wing closed and beak closed ( $r_{364} = 0.23$ ,  $p < 0.01$ ). No correlation existed when the correlation coefficient equalled  $-1$ , because this indicated exclusive behaviours that could not occur at the same time.

Mutually exclusive strong negative correlations with evidence for significance ( $p < 0.05$ ) (Table 2.2) exist between head up and beak closed ( $r_{364} = -0.66$ ); and head down and gular fluttering ( $r_{363} = -0.55$ ). Weaker significant negative correlations ( $-0.20 < r_{363} < -0.26$ ,  $p < 0.05$ ) exist between head down and sitting, wing closed and sitting, standing and gular fluttering, head up and standing, wings closed and standing and wings propped and gular fluttering.

### 2.3.3 Temperature and behaviour correlation

Observations on the behaviour of bank cormorants indicate that they did experience heat stress, but Spearman's correlations test yielded only one behaviour which was strongly positively correlated with  $T_e$ : gular fluttering ( $r_{184} = 0.67$ ,  $p < 0.01$ ). The head up behaviour and  $T_e$  were also correlated, but weak ( $r_{184} = 0.34$ ,  $p < 0.01$ ). Ambient temperature and gular fluttering were also positively correlated ( $r_{178} = 0.53$ ,  $p < 0.01$ ), but not as strongly as operative temperature and gular fluttering.

Selecting the model was based on AIC scores and the biological value of the behaviour that best described the results. Type 2 moult models (Erni *et al.* 2013) were used as the proportion of time spent gular fluttering and head up included both zeroes and ones (Figure 2.11).

### 2.3.4 Operative temperature and gular fluttering

The total number of observations included in the Underhill-Zucchini Moult Model was 366, of which 129 had no gular fluttering, 16 were gular fluttering continuously, and 221 had measured values of the percentage of time spent gular fluttering which were greater than 0% and less than 100% (Figure

2.12). Applying the model to these data, without any explanatory variables included, showed that the mean operative temperature at which gular fluttering was initiated was 21.0°C (SE 0.5°C), and that the standard deviation of the normal distribution describing the variability of the starting temperature of gular fluttering was 6.2°C (SE 1.8°C). The “duration” parameter was 13.2°C (SE 1.1°C). This indicated that the average bird gular fluttered continuously at temperatures above 34.2°C (calculated as 21.0+13.2). Expressed differently, for each 1°C increase in operative temperature between 21.0°C and 34.2°C, the estimated increase in the proportion of time spent gular fluttering was 0.076 (calculated as 1/13.2). Expressed as a percentage, there is an estimated 7.6% increase in time spent gular fluttering for each 1°C increase in operative temperature.

Once explanatory variables were introduced into the model (colony and breeding state, each with three levels), the model with the smallest AIC included both variables, but only for the starting temperature of gular fluttering (Figure 2.13). In this model, the “duration” parameter was 14.8°C (SE 1.4°C) and the standard deviation of starting temperature was estimated to be 6.5°C (SE 2.0°C). The most striking result was that once chicks were large woollies, the onset of gular fluttering was 6.2°C (SE 1.6) higher than it was during the incubation stage. This is a statistically significant difference ( $t = 3.9, p < 0.001$ ). In contrast, the onset of gular fluttering with small to medium woollies was 0.3°C (SE 0.8°C) lower than it was during the incubation stage, a non-significant difference ( $t = 0.33, n.s.$ ). There were differences between colonies; with Jutten Island as baseline, the start of gular fluttering at Robben Island was 1.9°C (SE 1.1°C) lower and at Stony Point was 4.0°C (SE 1.0°C) lower (Figure 2.13).

## 2.4 Discussion

This chapter provided two important results. Firstly, environmental temperature does affect the breeding behaviour of bank cormorants, increasing their thermoregulatory behaviours to cool down when heat stressed. Secondly, the main method of heat loss of the bank cormorant was gular fluttering, with the time spent gular fluttering increasing as their heat load increased.

### 2.4.1 Ambient and operative temperatures

Using black copper mounts, I observed, as predicted, that there was a correlation between the measured ambient temperature and the operative temperature at the nest site, both corresponding with the temperature of the environment (Bakken *et al.* 1985). This also explains that even with lower  $T_a$  the birds experienced a high  $T_e$  resulting in increased heat loads on the breeding bird. The temperatures also varied with the time of day, with higher temperatures being recorded for both  $T_e$  and  $T_a$  between 11h00 and 14h00.

Operative readings were better correlated to the behaviour of the bank cormorant than the ambient temperature, and this supports the decision to use operative temperature rather than ambient temperature in the study of thermoregulation of the bank cormorant. This means that operative temperature can be used to explain the relationship between thermal stress and environmental temperatures. This is similar to findings by Bakken *et al.* (1985) that operative temperature can be used with reliable accuracy.

#### 2.4.2 Thermoregulatory behaviour and increasing temperatures

Thermoregulatory behaviours of the bank cormorants demonstrate that they do experience temperatures that stress them and as expected they reacted to this heat stress with certain behavioural responses. Similarly, Kentish plovers *Charadrius alexandrinus* exhibit behaviours to promote heat loss at exposed nesting sites (Amat and Masero 2004). The bank cormorant's dark plumage also causes them to acquire a larger heat load than a lighter coloured bird species might (Hochscheid *et al.* 2002).

Gular fluttering (evaporative cooling) was the main thermoregulatory behaviour employed to reduce heat stress experienced by the bird while nesting; this was similar to many seabird species that employ evaporative heat loss through gular fluttering (Oswald and Arnold 2012). Gular fluttering promotes evaporative cooling from surfaces that would not normally be exposed to air flow, and this increases heat loss (Lasiewski and Snyder 1969). These results are similar to findings by Lasiewski and Snyder (1969) who found that even when double-crested cormorants *P. auritus* are exposed to low heat loads, they open their mouths and commence gular fluttering. A study on masked boobies (Bartholomew 1966) also found that gular fluttering was the most obvious action for heat loss while the birds were raising their young, employing it continuously while there was direct sunlight on the birds.

It is not clear why there were intercolony differences in the mean operative temperature at which gular fluttering started, with Stony Point having a 4°C lower threshold than the other two colonies. It is possible that at Stony Point, which is more sheltered from the prevailing winds during the breeding season, the effect of wind chill was less than at the other colonies on the West Coast.

This is the first application of the statistical model, custom-built by Underhill and Zucchini (1988) to estimate the parameters of primary moult, to another context (L.G. Underhill, pers. comm.). The statistical challenge is the same in both cases. There are observations made prior to the onset of moult/gular fluttering and observations after moult is complete/gular fluttering is continuous, and there is a third category of observations in which the response is continuous, i.e. a measure of the proportion of the way through moult/proportion of the time spent gular fluttering. Thus the application of the Underhill-Zucchini Moult Model is appropriate in this context.



Not only did the bank cormorants gular flutter when exposed to high heat loads, the amount of time spent gular fluttering increased as temperatures increased. The average bank cormorant starts to gular flutter at a  $T_e$  of 21°C and the mean observed  $T_e$  was 24.4°C. This temperature is close to the temperature at which African Penguins *Spheniscus demersus* start to gular flutter (24°C) (Frost *et al.* 1976). The time spent gular fluttering increased to 100% of the time when the average bird are exposed to operative temperatures were over 34°C. These results are similar to the results of a study done by Bartholomew *et al.* (1968), who found that (in a controlled experiment) as the heat load increased, the amount of time spent gular fluttering increased for double-crested cormorants, brown pelicans *Pelecanus occidentalis*, horned *Bubo virginianus* and barn owls *Tyto alba* and mourning doves *Zenaidura macroura*. Similar to the bank cormorant, under severe heat stress, gular fluttering was continuous (Bartholomew *et al.* 1968).

There was a correlation, albeit weak, between temperature increase and the “head up” behaviour, but there was also a correlation between the “head up” action and gular fluttering. This correlation could be of a result of the beak being more open when the bird is experiencing high heat loads (Lasiewski and Snyder 1969) and giving of the impression that the head is tilted backwards. This can similarly be seen with adult Heerman’s gulls *Larus heermanni*, extending their necks as the beak opens more widely for evaporative heat loss (Bartholomew and Dawson 1979).

#### 2.4.3 Thermoregulatory behaviour and the presence of eggs and chicks

Incubating is generally seen as a warming process (Downs and Ward 1997) and therefore it is likely that the bird will be hotter when on eggs or small chicks. This is similar to the results in this study, that an average bank cormorant starts to gular flutter at a lower temperature on eggs or small to medium sized chicks than when caring for larger chicks or fledglings. This is because older cormorant nestlings are better able to maintain their own constant body temperature during periods of heat stress and newly hatched chicks show little capacity of thermoregulation (Lasiewski and Snyder 1969). Similarly the younger chicks of the masked booby are completely dependent on their parents for protection from the physical environment (Bartholomew 1966).

## 2.5 Conclusions

The fact that bank cormorants nest in exposed breeding locations provided a great opportunity to examine the thermoregulatory behaviour of these birds; and evidence suggests that there is a link between increasing environmental temperature and increasing thermoregulatory behaviour to cool. However, for now the thermoregulatory capacity of the bank cormorant seems to be adequate to meet the thermal stress demands caused by high environmental temperatures. Like the masked boobies (Bartholomew 1966), their attachment to guarding their egg and chicks are remarkable, as they were never observed leaving the nest to cool down or find conditions where heat stress can be avoided.

Table 2.1. Observed behaviour of nesting bank cormorants at Robben Island, Jutten Island and Stony Point in 2012 and 2013

Code	Behaviour	Description
S	Sitting	Bird sits firmly on nest
C	Crouching	Bird raises body from egg(s) or chick(s)
ST	Standing	Bird is standing next to egg(s) or chick(s) and they are fully exposed
GF	Gular fluttering	Bird's mouth is open and air flow is experienced over the gular
BC	Beak closed	Bird's beak is closed
HD	Head down	Bird's head is held at a normal straight position
HT	Head tucked	Bird's head is tucked under its wing
HU	Head up	Bird's head is tilted up and backwards
WC	Wings closed	Bird's wings are closed and resting tightly on body
WP	Wings propped	Bird's wings are lifted from body and dropped to the side of the body

Table 2.2. Behaviour of nesting bank cormorants' correlation matrix. Values printed in italics indicate significant and meaningful positive correlations ( $r > 0.2$ ,  $p < 0.05$ ). The abbreviations for the observed behaviours are in Table 2.1. The correlation for gular fluttering (GF) and beak closed (BC) is  $-1$ , because those two activities cannot be done simultaneously. This also applies to wings propped (WP) and wings closed (WC)

	S								
C	-0.49	C							
ST	-0.76	-0.20	ST						
GF	0.15	0.08	-0.23	GF					
BC	-0.14	-0.9	<i>0.23</i>	-1	BC				
HD	-0.22	0.10	0.18	-0.55	<i>0.55</i>	HD			
HT	0.05	-0.14	0.05	-0.29	0.29	-0.14	HT		
HU	0.18	-0.01	-0.20	<i>0.66</i>	-0.66	-0.84	-0.41	HU	
WC	-0.06	-0.25	<i>0.26</i>	-0.23	0.23	0.09	0.16	-0.17	WC
WP	0.06	<i>0.25</i>	-0.26	0.23	-0.23	-0.09	-0.16	0.17	-1



Figure 2.1. Location of the three studied bank cormorant colonies during 2012 and 2013 along the western Coast of South Africa



Figure 2.2. The bank cormorant colony at Stony Point in 2013



Figure 2.3. The bank cormorant colony at Robben Island in 2013



Figure 2.4. The bank cormorant colony at Jutten Island in 2013



Figure 2.5. A black copper sphere and Stevenson's screen placed near the Robben Island colony



Figure 2.6. Cameras and recording equipment placed to record nests at the Jutten Island colony (similarly at Robben Island)



Figure 2.7. Example from video footage of nesting bank cormorant (bird on the left) displaying thermoregulatory behaviours: gular fluttering (GF), head up (HU), wings propped (WP), and crouching (C)



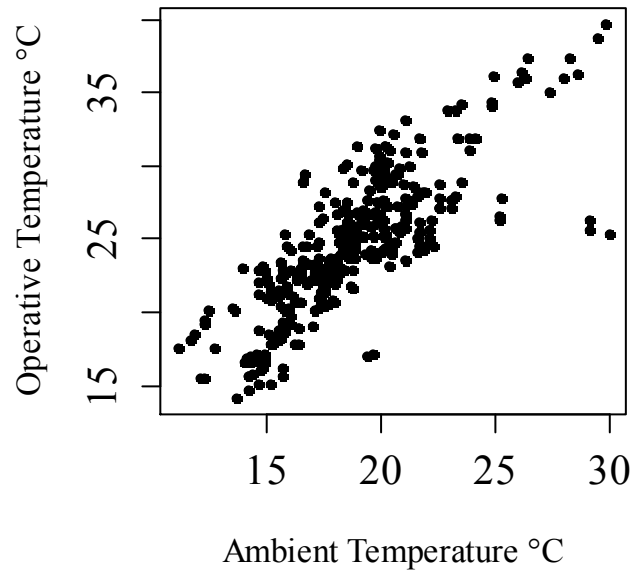


Figure 2.8. Relationship between ambient and operative temperature ( $r_{385} = 0.668$ ,  $p < 0.001$ ) at Robben Island, Stony Point and Jutten Island

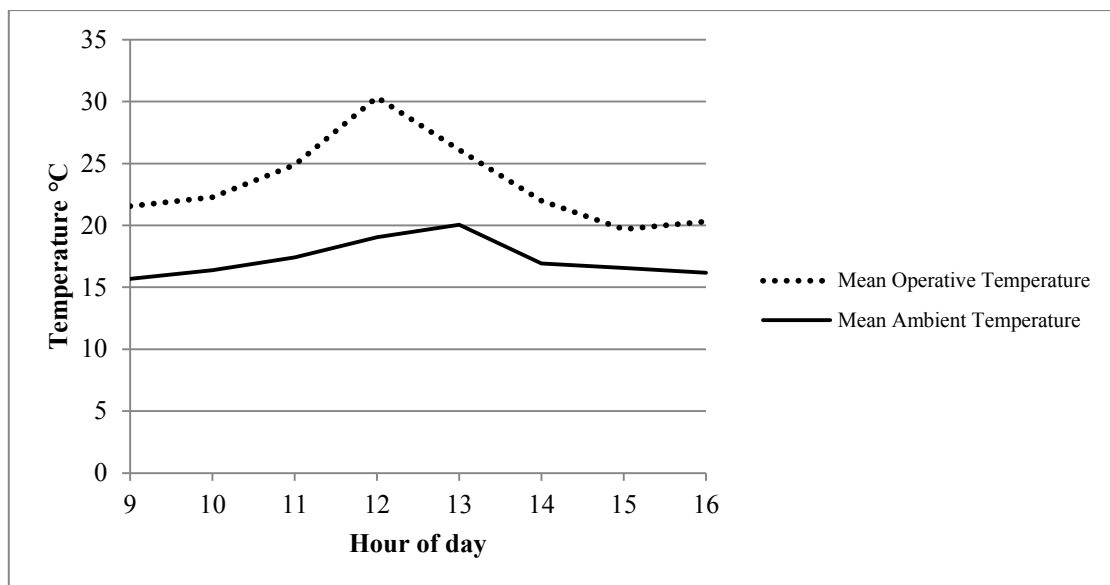


Figure 2.9. Mean operative and mean ambient temperatures recorded during each hour of the day. Robben Island, Stony Point and Jutten Island obtained during 201 and 2013 have been combined

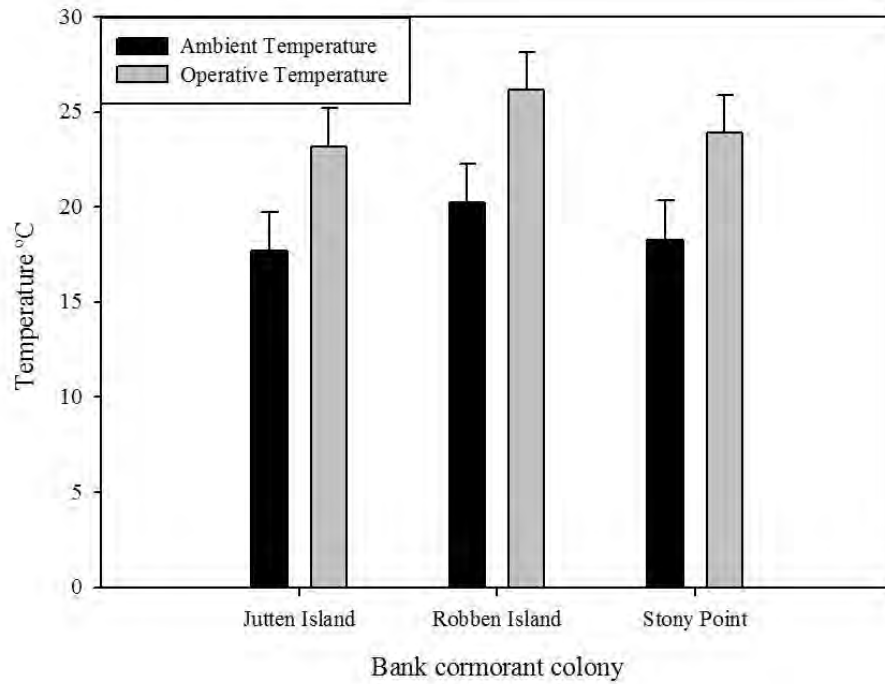


Figure 2.10. Average ambient and operative temperature measured at the same time at different colonies (with 95% confidence intervals) during 2012–2013. At each locality ambient temperatures were 5–6°C than operative temperatures

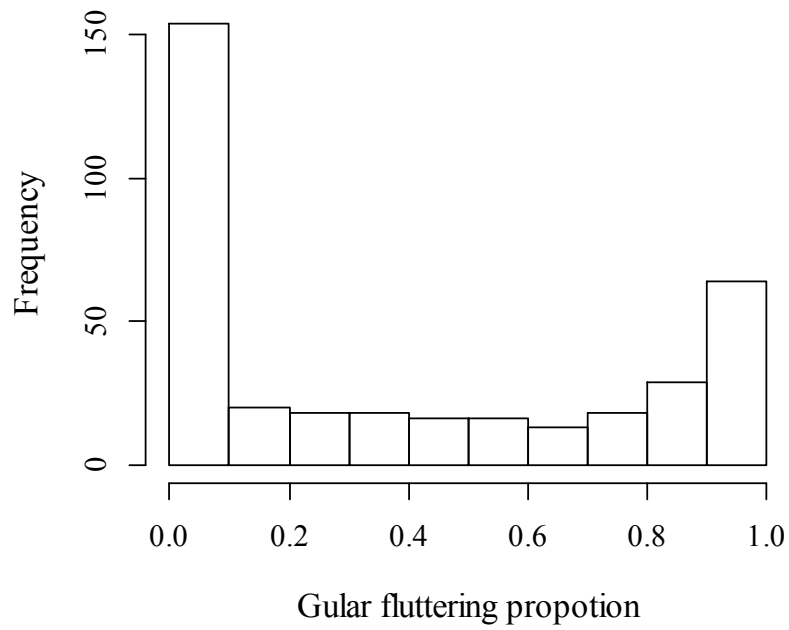


Figure 2.11. Histograms displaying frequency of proportion of bank cormorants observed gular fluttering and with head up behaviour simultaneously

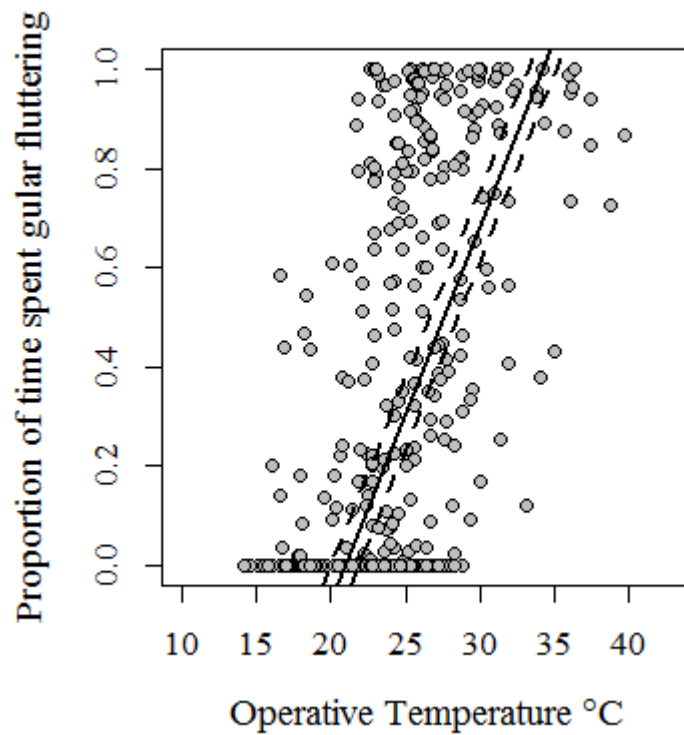


Figure 2.12. Relationship between the proportions of time bank cormorants spent gular fluttering and operative temperature at the nest, using the Zucchini-Underhill Moulting Model. At  $y = 0$ , the solid line represents the operative temperature at which the average bank cormorant starts to gular flutter. At  $y = 1$ , the solid line represents the temperature at which 50% of the cormorants are gular fluttering continuously. The dashed line indicates the 95% confidence intervals of the mean starting temperature

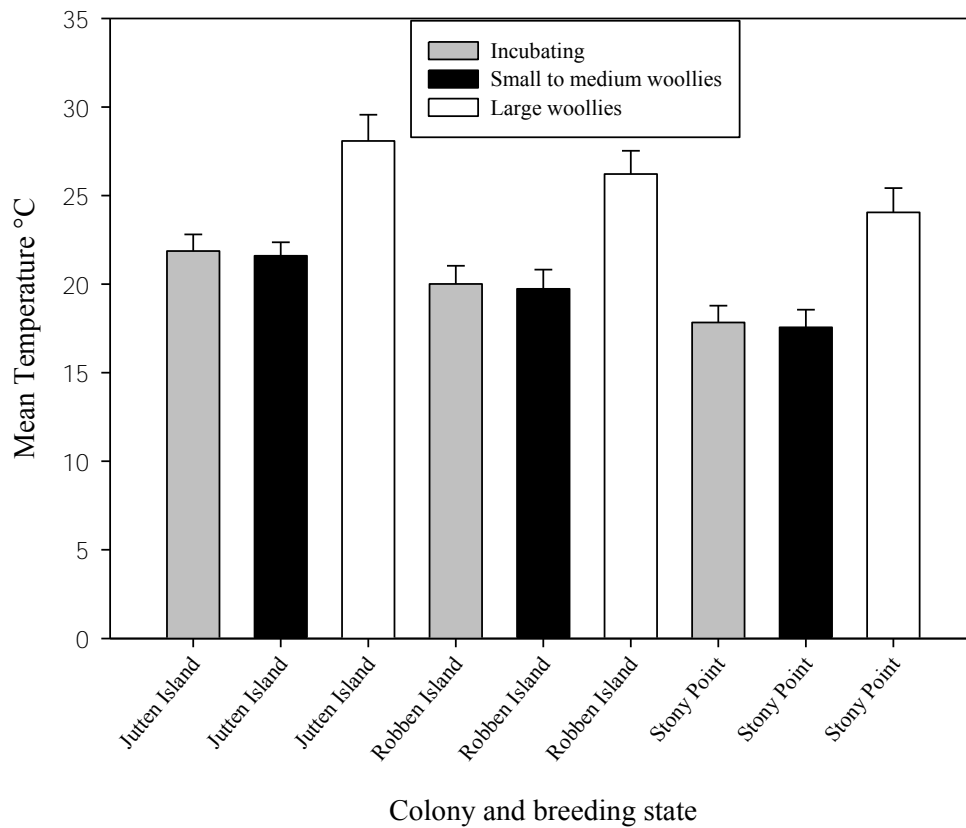


Figure 2.13. The relationship between the mean starting temperatures of gular fluttering in bank cormorants for the three classified breeding states as shown in the legend at Robben Island, Stony Point and Jutten Island

## Chapter 3

### **The influence of possible environmental variables on the breeding productivity of the ‘Endangered’ bank cormorant *Phalacrocorax neglectus* in the Western Cape, South Africa**

#### **3.1 Introduction**

Breeding success of certain seabirds is affected by the physical environment (Mallory *et al.* 2009b). Extreme weather conditions, such as high temperatures and storm activity, have the potential to decrease the breeding productivity of a bank cormorant colony, because the breeding performance of seabirds is impacted by weather conditions (Chastel *et al.* 1993). This topic has now received considerable attention in the field of climate change research (Ramos *et al.* 2002). Extreme environmental conditions, such as these mentioned above, may have stronger effects on population dynamics than average climate (Moreno and Møller 2011). In addition it has been suggested that the increased frequency of storms and extreme heat also lowers the reproduction output of seabirds, through hypothermia, hyperthermia and even starvation and predation in chicks (Boersma and Rebstock 2014).

The bank cormorant *Phalacrocorax neglectus* is classified as ‘Endangered,’ following a decline in its overall breeding population from c. 9000 breeding pairs between 1975 and 1981 to c. 3000 pairs in 2011 (Crawford *et al.* 2008a, 2012, BirdLife International 2013). This represents a decline of over 60% in the 40 years leading up to 2011. The bank cormorant is endemic to the Benguela upwelling system off the coast of south-western Africa (Crawford *et al.* 2008a) and at the start of the 21<sup>st</sup> century its breeding distribution ranged from Swakopmund (22°41' S, 14°32' E), central Namibia, in the north, to Quoin Rock, in the east (34°47' S, 19°40' E), Western Cape, South Africa (du Toit *et al.* 2003).

Many breeding seabirds along the African coastline are threatened by disturbance and terrestrial predators; choice of breeding location is further limited by the availability of food resources close by (Berruti *et al.* 1995, Randall 1995, du Toit *et al.* 2002, Bartlett *et al.* 2003). The study species, bank cormorant, is particularly sensitive to anthropogenic disturbance during the breeding season (Cooper 1981). Therefore, breeding colonies occur mostly on offshore islands, high offshore rocks and boulders and man-made breakwater structures (du Toit *et al.* 2002, Bartlett *et al.* 2003). Colonial seabirds, such as the bank cormorant, tend to make excellent study subjects for determining the relationship between environmental conditions and breeding success; because nests are concentrated at the colonies and usually the environmental variables are easy to measure (Nettleship 1972).

Bank cormorants construct large, heavy nests, engineered mainly from wet seaweed, on rocky surfaces near the water’s edge (Cooper 1986). This leaves them exposed to weather and sea conditions, and it has been found that whole nests and all their content can be lost during storms

(Crawford and Cooper 2005, Sherley *et al.* 2012). It has been shown that the quality and location of a breeding site can influence the breeding success of a seabird species (Chastel *et al.* 1993). Durant *et al.* (2004) also found that many seabird populations in the North Atlantic Ocean were affected by weather conditions, especially storms, through egg and/or chick mortality, affecting their breeding success. Understanding the variability in breeding success of the bank cormorant is important for managing the declining population, because weather variables can greatly influence reproduction of animal populations (Ramos *et al.* 2002)

Building on previous observations by Sherley *et al.* (2012), this chapter presents a study on the effects of weather variability and changes in sea state on the nesting survival of breeding bank cormorants, and seeks to determine the factors influencing the survival of eggs and chicks (Ramos *et al.* 2002). The effects of these environmental parameters were tested on the breeding success at three breeding colonies along the coast of the Western Cape, South Africa: Robben Island, Jutten Island and Stony Point.

## **3.2 Materials and methods**

### **3.2.1 Study sites**

During the austral winters of 2012 and 2013 I studied the breeding success of three bank cormorant colonies in the Western Cape, South Africa (Figure 3.1). The study was undertaken at Robben Island (33°48' S, 18°22' E), Stony Point (34°22' S, 18°43' E) and Jutten Island (33°05' S, 17°57' E). Robben Island is situated in Table Bay, Cape Town, whereas Jutten Island is located c. 90 km north-west of Cape Town, just outside the mouth of Saldanha Bay on the West Coast. Stony Point is a mainland colony on a rocky point at Betty's Bay.

### **3.2.2 Data collection**

At the three breeding colonies unmarked breeding bank cormorants were studied during 2012 and 2013 (Table 3.1). Colonies at Stony Point and Robben Island were visited weekly in 2012, or as often as sea and weather conditions permitted. During 2013, the aim was to visit Stony Point and Robben Island every two weeks, alternating between Jutten Island trips. The Jutten Island colony was visited every three weeks in 2012 and every two weeks in 2013. During 2012 nest checks at Robben Island started on 11 April and finished on 13 August. In 2013 nest checks started on 25 March and ended on 5 September. At Stony Point nest checks were made from 9 May 2012 to 7 September 2012 and 12 March 2013 to 2 September 2013. Jutten Island was monitored from 23 May to 12 September in 2012 and 15 April to 26 August during 2013. This coincided with the main breeding season (May–October) of the bank cormorant in the Western Cape (Crawford *et al.* 2008).

During each visit to a colony, information was collected. Observations were made 30–60 m from the colonies with the use of binoculars and telescopes, to avoid disturbance of breeding birds. Nests were manually identified and numbered on photographs taken at fixed locations, at the start of the season; this enabled individual nests to be identified with certainty on subsequent visits (Sherley 2010) (See Chapter 2, Figures 2.2, 2.3 and 2.4). When new nests appeared they were numbered accordingly and added to new photographs from the same fixed locations. Nests observed only one visit were excluded from the analysis. To my knowledge, no birds were disturbed during observations.

On each visit, the state of the nest and the stage of the breeding attempt of bank cormorant nests were recorded, in these categories: building/guarding nest (potential nesting position), incubating eggs or rearing of chicks. On these visits, the number of eggs and/or chicks were recorded for each nest as well as the size of the chick. Chick sizes were divided into five categories (Sherley *et al.* 2012): hatchling – less than six days old and no down (B1), small downy – less than half the adult's size and sheltering under the adult (B2); medium downy – larger than half the adult's size but less than three-quarters and covered in down (B3); large downy – larger than three-quarters of the adult's size and still covered in down (B4); and woolly necks – fully grown to the size of the adult with down on the neck and head, but flight feathers on the body (B5). For each nest the number of eggs hatched and the number of chicks fledged was calculated. A chick was regarded as fledged when it was seen to have lost all of its down.

Nest checking started at the start of the breeding season (when active nests were identified) and ended when all monitored juveniles had fledged. Clutch size proved difficult to determine both because many nests were too deep to see the eggs (from the observation distance) and because eggs were not always visible due to incubating adults. I continued monitoring nests both after successful and failed breeding attempts, in order assess whether the birds returned for a second breeding attempt.

These data along with climate and sea state data, were used to determine a relationship between nesting success of bank cormorants and environmental parameters. These data were used to determine the breeding success of the bank cormorant over this two year period and compared with the breeding success results obtained by Sherley *et al.* (2012). Climate data (temperature (°C), wind (km/h) and rainfall data (mm)) were supplied by the South African Weather Services (SAWS). These data included hourly and daily measurements for weather stations at Cape Town (33°58' S, 18°36' E), used for Robben Island, Hermanus (34°25' S, 19°13' E), used for Stony Point, and Langebaan (32°58' S, 18°09' E), used for Jutten Island.

Sea state data were obtained from the Council for Scientific and Industrial Research (CSIR), Stellenbosch, and collected on behalf of the Transnet National Port Authority (TNPA). The data used were captured in three hourly intervals, starting from 00h00 to 21h00 daily. Data captured were significant wave height (m), spectral peak wave period (sec) and peak wave direction (degrees). The



Cape Point station (CP01) (34°12' S, 18°16' E) was used to provide data for Robben Island and Stony Point and the Saldanha Bay station (SB01) (33°02' S, 17°58' E) was used to provide data for Jutten Island.

### 3.2.3 Statistical analysis

#### *Incubation and chick rearing success*

To account for possible bias introduced by not monitoring all nests from the start of incubation, nest success was determined using a combination of the Mayfield (1961, 1975) method and parametric survival analysis (Sherley *et al.* 2012). Nesting success for the incubation and chick rearing (brooding) period was determined using the Mayfield (1961, 1975) method. All breeding attempts reaching a conclusion (fledged or failed) were considered in determining nesting success at the colonies. Incubation success was determined using hatching success. Because clutch size could not be determined, the nest content was considered to have survived the incubation period if at least one chick hatched and the chick rearing period if at least one hatched chick fledged (partial failure were ignored by models). Nest days (number of days on eggs or chicks) were calculated using the method of taking the mid-point between visiting days (Mayfield 1961).

The survival models were implemented in the modelling software package R v.3.0.3 (R Development Core Team 2009). The 'survreg' function was used to determine the daily failure rate of a nest and the survival probability of a nest and its contents during the incubation or chick rearing period. Following Sherley *et al.* (2012) the maximum likelihood estimate of risk of failure (F) per sampling interval, for nests with eggs or chicks, was defined as:

$$F = \exp(-\alpha - \beta)$$

where  $\alpha$  and  $\beta$  (intercept and slope) were the estimated parameters from the calculated regression. Using this formula, nest survival (S) was defined as:

$$S(t) = \exp(-\alpha - \beta x) t$$

Where, again,  $\alpha$  and  $\beta$  (intercept and slope) were the estimated parameters from the calculated regression and  $x$  was the value of any continuous explanatory variable (fixed at  $x = 1$  for factorial variables for a model with one explanatory variable) at any time  $t$  (days). To make these result comparable to those of Sherley *et al.* (2012), the incubation period was taken as 30 days and the chick rearing period as 55 days (Cooper 1987).

Using the colony and year as explanatory variables (e.g. Robben 2013) in the model, nest success values were then compared between the three studied colonies and older data for breeding success at Robben Island and Mercury Island (Sherley *et al.* 2012)

### *Relationship between climate and sea-state variable and nest success*

Nest failure events for the incubation and brooding period at Robben Island, Jutten Island and Stony Point were related to weather and sea state data using generalised linear models with a binomial error distribution and a logit link function. Environmental parameters that were found to be correlated with the probability of nest failure were included in models. Models were run in R and the best fitting model was selected using AIC scores (Burnham and Anderson 2002). The response variable was the proportion of failed nests during a visit interval and the explanatory variables were the mean, total, maximum or minimum of climate and sea state variables. Number of days in the visiting interval, year, and colony were included in the candidate model set.

### **3.3 Results**

Natural year-to-year variation in survival of the bank cormorant will be observed. Particularly pronounced variation in the survival of the bank cormorant might be explained by environmental parameters affecting the survival of the species. The relationship between survival and environmental parameters was explored separately for the two phases of breeding: incubation and chick rearing (brooding and past brooding). A total of 162 bank cormorant pairs were studied during 2012 and 2013 (Table 3.1). There was interannual and intercolony variation in the properties of nests at which at least one chick fledged (Table 3.2) and reproductive failure occurred at all colonies during both study years. The percentage of nests with one successful fledgling was highest at Robben Island during 2012 and lowest at Stony Point in 2012 (Table 3.2). The larger number of nests monitored in 2013 at Robben and Jutten Islands, was not due to more nests at the colonies, but rather due to more nests being visible and increased experience of the observer.

#### 3.3.1 Incubation success

The daily failure rate for bank cormorant nests at Robben Island during the study (2012 and 2013 combined) for the incubation period was 0.004 (0.0013 SD). Jutten Island had a higher daily failure rate during incubation of 0.006 (0.0017 SD) and Stony Point displayed a daily failure rate of 0.005 (0.0027 SD).

The probabilities of a bank cormorant nest surviving (from laying to fledging) during 2012 and 2013 for Robben Island, Jutten Island and Stony Point did not differ greatly (Table 3.3 and Figure 3.2). The lowest observed value for survival probability was on Robben Island in 2009 and was 0.54 (95% CI: 0.41–0.7), after a steady decline in the success of breeding bank cormorants since 2007 (0.68, 95% CI: 0.55–0.85). The 2009 value was significantly different from the survival probability of 2011, 2012 and 2013 for Robben Island (2011: 0.86, CI: 0.7–1) ( $p < 0.05$ ).

### 3.3.2 Chick rearing success

The daily bank cormorant failure rates for 2012 and 2013 combined during chick rearing for Robben Island, Jutten Island and Stony Point were 0.0045 (0.0011 SD), 0.0046 (0.002 SD) and 0.0074 (0.002 SD) respectively. Stony Point's daily failure rate was the highest and Robben Island was the lowest.

In contrast to incubation success, Stony Point displayed the lowest survival probability for the years 2012 of 0.64, (95% CI: 0.46–0.89) and 2013 of 0.68, (95% CI: 0.51–0.91) when compared with Robben Island and Jutten Island (Table 3.4 and Figure 3.3). Robben Island seemed relatively stable with the exception of a low survival probability in 2009 (0.51, CI: 0.3–0.87) – the lowest of all the observed survival probabilities. Jutten Island's survival decreased from 2012 (81.93%) to 2013 (73.46%), though not significantly.

### 3.3.3 Environmental variables: weather and sea state data

Although temperatures reached a high of over 37 °C (Table 3.5), similar to that of the body temperature range of bank cormorants, 37.4–40.0°C (Wilson and Grémillet 1996), it did not seem to have an effect on the reproductive success of the bank cormorant. The daily minimum temperatures ranged between 1.4°C and 14.1°C (Table 3.5). The maximum total rainfall occurring during a visiting period was over 100 mm and some periods experienced no rainfall at all; the mean total rainfall was 21.5 mm during a visiting interval (Table 3.5).

### 3.3.4 Incubation success and environmental variables

The probability of failure (PF) of an incubating nest (failed nests/active nests in a period) was found to be correlated with some of the tested environmental factors. PF was positively correlated with days during visiting intervals ( $r_{55} = 0.2$ ,  $p > 0.5$ ), maximum rain ( $r_{55} = 0.25$ ,  $p > 0.5$ ), maximum wave height ( $r_{55} = 0.23$ ,  $p > 0.5$ ). It was negatively correlated ( $r_{55} = -0.21$ ,  $p > 0.5$ ) with the mean maximum temperature. PF was also positively correlated with the total rainfall ( $r_{55} = 0.33$ ,  $p = 0.01$ ) and the maximum wind gust ( $r_{55} = 0.39$ ,  $p = 0.002$ ). No difference was found between the three colonies and therefore colonies as a variable was excluded from the model.

When significant factors were included in the generalised linear models (Table 3.6), the best model to describe the probability of nest failure for bank cormorants during the incubation period included both days and the maximum wind gust as explanatory variables (Figure 3.7). This model explained 21.1% of the total deviance in nest survival during incubation.

Figure 3.7 shows the model visually, as the maximum wind gust increased, then the probability of failing during incubation would have increased. It also shows that the longer the visiting interval, the higher the risk of the nest not being present on the next nest check. When a nest is checked after 30

days during the incubation period and the wind gust is at maximum speed, there is a 0.6 probability (60%) of the nest not being there; this probability lowers as the visiting interval and wind gust speed decreases (Figure 3.4).

### 3.3.5 Chick rearing success and environmental variables

The environmental parameters that showed significant correlation ( $r > 0.20$  and  $p < 0.05$ ) with the probability of failure during bank cormorant chick rearing were mean maximum temperature °C ( $r_{50} = -0.34$ ); maximum daily rainfall mm ( $r_{50} = 0.29$ ); mean daily rainfall mm ( $r_{50} = 0.28$ ); total rainfall mm ( $r_{50} = 0.30$ ) and maximum wind gust km/h ( $r_{50} = 0.41$ ). Maximum daily temperature °C and maximum wave height m were also positively correlated with the probability of failure, but with p-values larger than 0.05. The interval interval visits to the nest sites was not correlated to probability of failure and was excluded from the models. Likewise, the colony had no influence, and this variable was also excluded.

The generalised model selection was based on models that returned the smallest AIC scores. These were two separate linear models with the explanatory environmental parameters, maximum wind gust speed (km/h) (AIC = 68.8) and maximum wave height (m) (AIC = 70.15) (Figure 3.5). Both these variables showed that an increase in the variable caused an increase in the risk of nest failure during the chick rearing period.

When the maximum wind gust increased to over 24 km/h, a nest with chicks had a 9% chance of failing. The same happens when the maximum wave height reaches over 6 m in height. A bank cormorant nest with chick(s) then had an almost 9% risk of chicks dying and the nest failing.

## 3.4 Discussion

Breeding success of bank cormorants are reduced through the loss of eggs or chicks during the breeding period (Weimerskirch *et al.* 2000). As predicted, there is no significant difference in overall nest success between the three studied colonies during the contrasted seasons in 2012 and 2013. However, it is well-recognised that marine bird reproductive performance can vary inter-annually (Sydeman *et al.* 2001) as a result of cyclic variations in oceanographic parameters (Weimerskirch *et al.* 2000). Stony Point had the lowest success during the chick rearing period, but was significantly different from the colonies. Robben Island had the highest reproductive success during the incubation period and Jutten Island showed a decrease in success from 2012 to 2013. This lack of statistical significance could be because the colonies show no significant short-term variation in environmental parameters (Suryan and Irons 2001) and the reproductive success may be correlated with the breeding population size of the researched years, a component that lacks in this study (Nur and Sydeman 1999). Small variability in breeding success has been reported numerous times for seabird studies, and this

variability can be influenced by a range of factors: parasites and disease, human interference and disturbance and changes in prey abundance and/or quality (Sherley *et al.* 2012). Chastel *et al.* (1993) also explained that weather conditions can be responsible for variability in breeding success (e.g. snowfall influences the breeding success of snow petrels).

When these differences in breeding success for the incubation and chick rearing period were tested against environmental parameters, there was no difference between the colonies, but consistent with our predictions, some environmental factors may be responsible for reproductive failure at the three studied nest locations. This is consistent with previous findings that weather conditions may affect seabird breeding conditions (e.g. Jouventin and Weimerskirch 1991, Chastel *et al.* 1993). However unlike what I expected, high temperatures did not seem to affect reproductive success during incubation or brooding as shown in the findings of Sherley *et al.* (2012). This lack of high temperatures influencing the bank cormorant's breeding success suggests that the bird is capable of incubating and rearing a chick successfully in spite of high environmental temperatures. Rather, strong wind and wave action seemed to be the main factors causing nest failures during the breeding of the bank cormorant.

Weather might not always affect adults, but still can influence fledgling success (Baird 1990, Durant *et al.* 2004), by causing egg or chick mortality (Sherley *et al.* 2012). The low breeding success during 2009 at Robben Island was as a result of two major storm events during the peak breeding season (Sherley *et al.* 2012). This provides evidence that environmental variables do influence the nest success of the bank cormorant.

During incubation, strong wind gusts were the only variable responsible for nest failure, and during chick rearing, it was the wind factor and the action of waves (significant wave height) at the colony that affected survival of chicks. Wind accompanied with other weather such as rainfall or increased wave action might be responsible for eggs being lost during the bad weather (Mallory *et al.* 2009). Chick loss related to wind is consistent with findings by Frederiksen *et al.* (2008) and Aebischer (1999) who suggested that gale winds and associated heavy rainfall during the breeding season could cause mortality amongst shag chicks, presumably through hypothermia. These effects are most pronounced when nests are exposed to these elements, as seen at bank cormorant breeding sites. Wind storms in the Arctic have also been shown to increase nest failure for northern fulmars breeding in the Arctic (Mallory *et al.* 2009a).

Sherley *et al.* (2012) showed that nest failures were related to the height of waves. This is consistent with my findings, that the maximum significant wave height decreased the survival probability of nests at three colonies. This is most likely because bank cormorants nest close to the water (Cooper 1986). Stony Point, the mainland colony, showed lower success during brooding, suggesting that nest failure happens mostly during the chick rearing period rather than during incubation. Most likely this

breeding location will be affected by wave action more than the other colonies, as it is more exposed to the ocean and incoming waves and therefore less sheltered from the impact of waves (pers. obs.), similar to exposed shag nests resulting in more juvenile mortalities (Frederiksen *et al.* 2008). The effect of wave action, however, was only apparent during brooding. Chicks can be washed away, drown or die as a result of hypothermia as a result of being splashed by the cold water.

### **3.5 Conclusions**

This study suggests that certain environmental variables influence the reproductive productivity of the bank cormorant, and that extreme weather events may cause breeding failures, because adults may not breed or fail at a breeding attempt (Moreno and Møller 2011). Given the nature and the cause of egg and chick mortality in this study, I predict that extreme environmental events such as increased wave height and wind speed will to be the main environmental variables responsible for nest failures during the breeding season of the bank cormorant. The predicted climate change models suggest that the frequency of these extreme events will increase, resulting in lower reproductive output for the bank cormorant. Understanding the influence of these environmental parameters on the nesting success of the bank cormorant will be important in understanding the population dynamics of the bank cormorant, and therefore the survival of the species.

The information provided by reproductive success studies can indicate which life history trait (stage) is mostly responsible for changes in reproductive performance (Sydeman *et al.* 2001); in this case it is the chick rearing period, the stage affecting fledgling success. This suggests that environmental variation does have an influence on breeding success, but this low breeding success can be possible as the bank cormorant is a long-lived marine bird species (Chastel *et al.* 1993). It is been suggested that birds are less likely to increase their effort in raising young when it may risk their own survival (Durant *et al.* 2004). Therefore, if weather conditions make it too difficult for parents to raise their young, or even finding food (Baird 1990, Durant *et al.* 2004), they might abandon their breeding attempt. Poor feeding conditions can be responsible for low reproductive success and the lack of food availability can be related to poor environmental conditions (Baird 1990). I suggest further research into the combined effect of climatic variation and food resource availability on the breeding success of the bank cormorant to better understand the variation in reproductive success.



Table 3.1. Number monitored of bank cormorant nests at three breeding locations in the Western Cape, South Africa during 2012 and 2013.

<b>Colony</b>	<b>2012</b>	<b>2013</b>	<b>Total</b>
Robben Island	41	40	81
Stony Point	24	23	47
Jutten Island	18	16	34
<b>Total</b>	<b>83</b>	<b>79</b>	<b>162</b>

Table 3.2. Hatching fledgling and breeding success of bank cormorants during 2012 and 2013 at three colonies in the Western Cape, South Africa. Successful nests were those of which at least one chick fledged

<b>Colony</b>	<b>Year</b>	<b>No. of nests monitored</b>	<b>No. of chicks hatched</b>	<b>No. of chicks fledged</b>	<b>Percentage of successful nests</b>
Robben Island	2012	38	46	38	82.61
Robben Island	2013	54	64	45	70.31
Jutten Island	2012	12	21	16	76.19
Jutten Island	2013	15	27	17	62.96
Stony Point	2012	23	23	13	56.52
Stony Point	2013	20	33	23	69.70



Table 3.3. Survival probabilities with 95% confidence intervals for four bank cormorant colonies during the incubation period, in southern Africa, during various breeding seasons: 2005, 2007–2013

<b>Colony and Year</b>	<b>Survival Probability</b>	<b>Upper 95 % CI</b>	<b>Lower 95% CI</b>
Mercury Island '05	0.713	0.811	0.626
Mercury Island '08	0.730	0.856	0.622
Mercury Island '10	0.839	0.912	0.772
Robben Island '07	0.680	0.846	0.547
Robben Island '08	0.568	0.743	0.433
Robben Island '09	0.536	0.695	0.413
Robben Island '11	0.860	1	0.699
Robben Island '12	0.890	0.986	0.806
Robben Island '13	0.899	0.998	0.809
Jutten Island '12	0.861	1	0.699
Jutten Island '13	0.810	1	0.638
Stony Pont '12	0.817	0.996	0.671
Stony Point '13	0.899	1	0.798

Table 3.4. Survival probabilities with 95% confidence intervals for four bank cormorant colonies during the chick rearing period, in southern Africa, during various breeding seasons: 2005, 2007–2013

<b>Colony and Year</b>	<b>Survival Probability</b>	<b>Upper 95 % CI</b>	<b>Lower 95% CI</b>
Mercury Island '05	0.819	1	0.622
Mercury Island '08	0.735	1	0.518
Mercury Island '10	0.740	0.862	0.635
Robben Island '07	0.963	1	0.895
Robben Island '08	0.855	0.947	0.772
Robben Island '09	0.761	1	0.559
Robben Island '11	0.860	1	0.698
Robben Island '12	0.509	0.874	0.296
Robben Island '13	0.814	1	0.613
Jutten Island '12	0.776	0.936	0.643
Jutten Island '13	0.786	0.928	0.665
Stony Pont '12	0.644	0.892	0.465
Stony Point '13	0.684	0.906	0.516

Table 3.5. Summary statistics for measured environmental parameters: temperatures (°C), rainfall (mm), wind (km/h) and wave action (m and sec)

<b>Variable</b>	<b>Minimum</b>	<b>Maximum</b>	<b>Mean</b>	<b>Standard Deviation</b>
Maximum temperature (°C)	17.50	37.30	23.74	4.39
Mean max temperature (°C)	15.92	28.02	19.16	2.59
Minimum temperature (°C)	1.40	14.10	6.97	2.79
Mean min temperature (°C)	5.47	15.43	9.97	2.14
Total rainfall (mm)	0	101.0	21.52	20.15
Maximum rainfall (mm)	0	34.4	10.29	8.58
Mean rainfall (mm)	0	14.4	4.62	3.22
Maximum wind gust (km/h)	10.10	24.6	17.44	3.75
Maximum significant wave height (m)	1.50	6.80	4.43	1.32
Mean peak wave period (sec)	2.82	14.01	11.94	1.56

Table 3.6. Candidate models of probability of failure of bank cormorant nests during incubation with various environmental parameters for incubation success

<b>Environmental parameters</b>	<b>AIC score</b>
Visiting days	112.4
Days and maximum wind	<i>107.4**</i>
Days and total rain	107.6
All parameters	109.1
Days, minimum temperature, mean minimum temperature	111.9
Maximum wind	113.3
Days and minimum temperature	114.1
Days and mean minimum temperature	109.9
Total rain	112.4

\*\*Chosen model with smallest AIC score



Figure 3.1. Locations of the three studied breeding bank cormorant colonies off the coast of South Africa

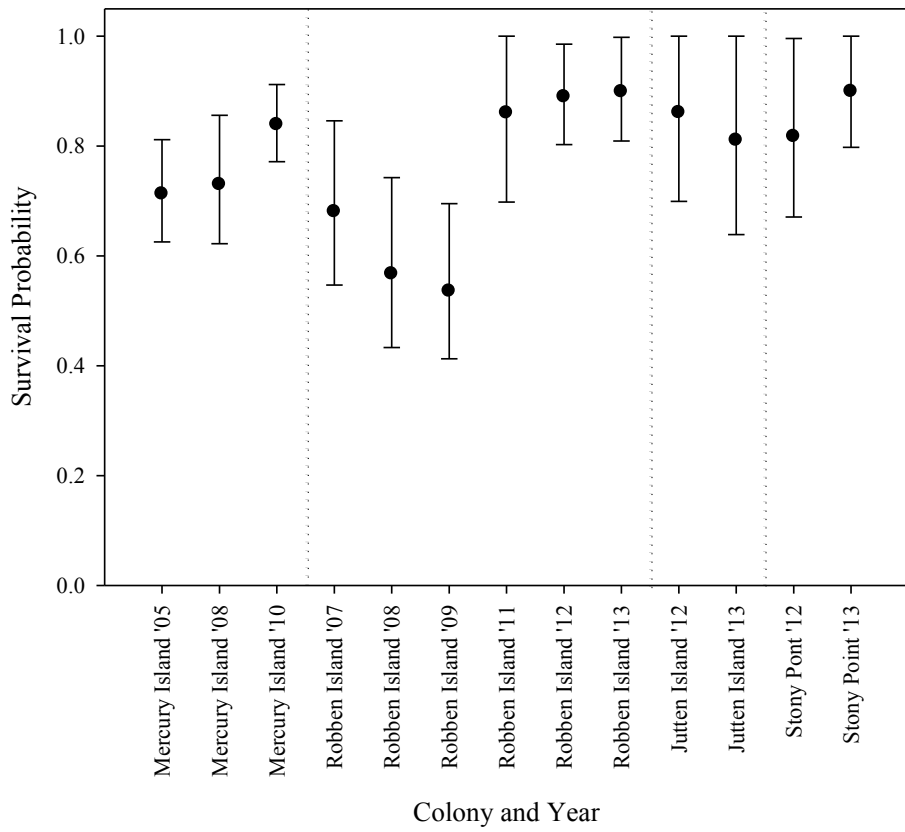


Figure 3.2. Incubation success with 95% confidence intervals for four bank cormorant colonies in southern Africa, during various breeding seasons: 2005, 2007–2013

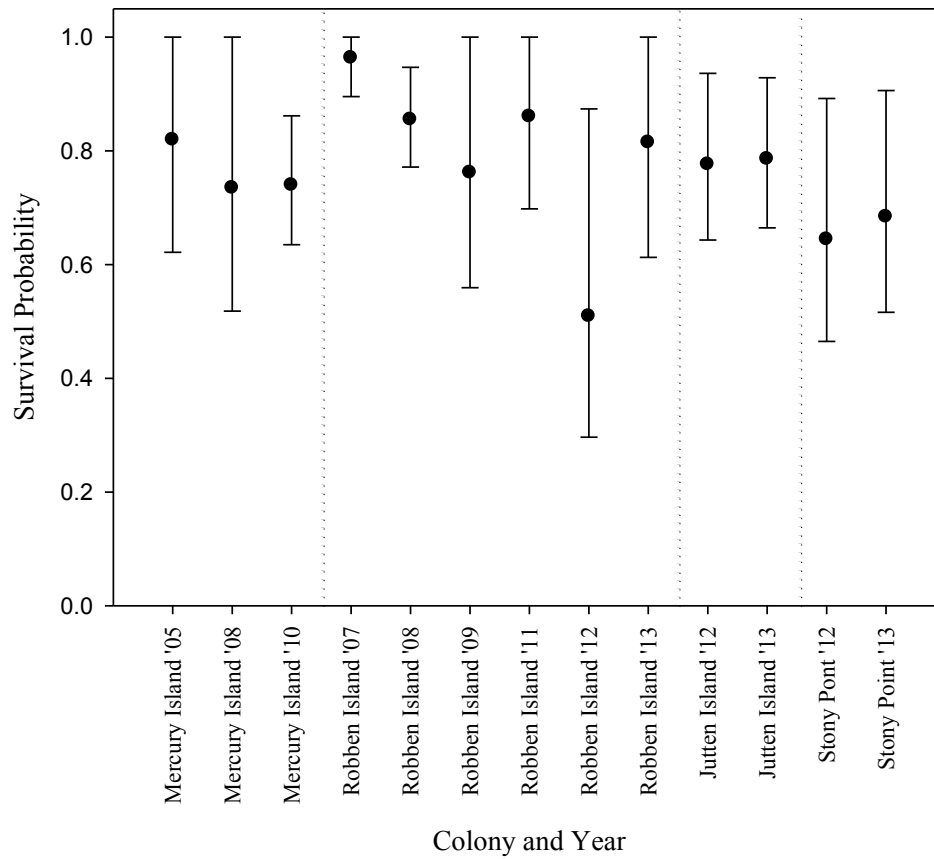


Figure 3.3. Chick rearing success with 95% confidence intervals for four bank cormorant colonies in southern Africa, during various breeding seasons: 2005, 2007–2013

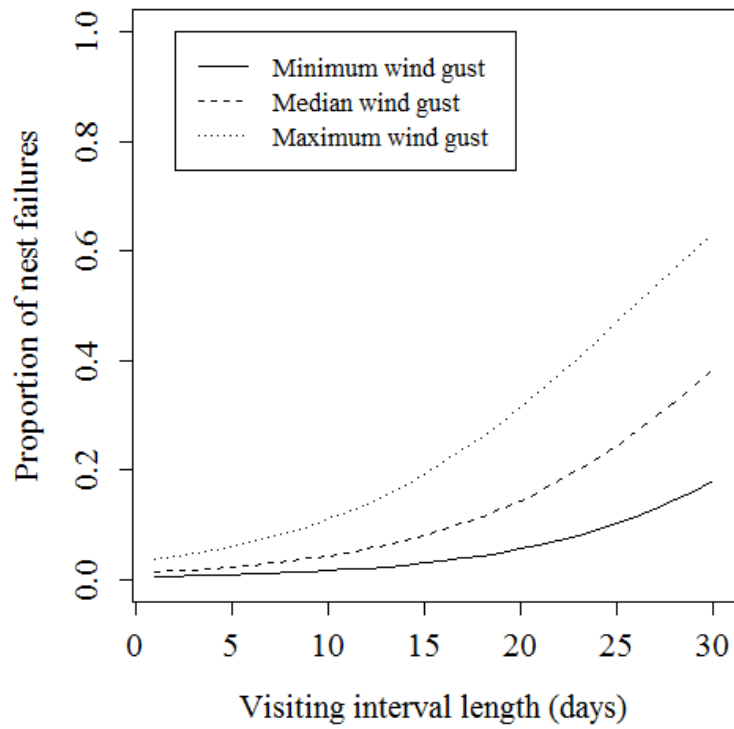


Figure 3.4. The relationship between increasing the proportion of nest failures and increase the in visiting interval for different levels of wind gusts: maximum wind gust values: min: 10.1 km/h; med: 17.5 km/h; max: 24.6 km/h



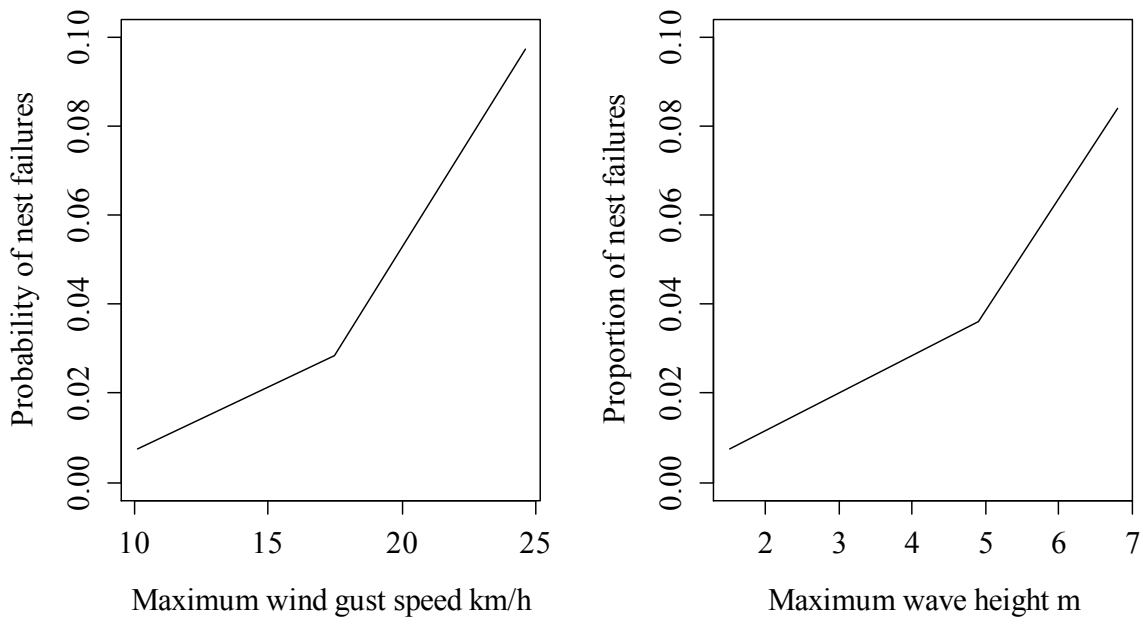


Figure 3.5. The linear relationship of the influence of increased wind gust speed ( $p < 0.05$ ) and maximum significant wave height ( $p < 0.05$ ) on the probability of nest failure during chick rearing for breeding bank cormorants

## Chapter 4

### Trends in the bank cormorant *Phalacrocorax neglectus* population of the Western Cape, South Africa: the impact of climate change

#### 4.1 Introduction

Climate monitoring and long-term climate reconstruction over the past decades indicate that the earth is warming (IPCC 2007). Ecologists face the challenge of predicting its impacts on species and communities (Hughes 2000). Wide spread climatic variation over inter-annual and longer periods has been shown to affect seabird populations (Bunce *et al.* 2002). Climate can affect seabird populations directly through changes in physiology or indirectly, by influencing the availability of a species' prey (Durant *et al.* 2004). Documented impacts of climate change on seabirds include changes in species demography and ranges, species abundance, phenology, breeding proportion, breeding success and adult survival (Crick 2004, Lemoine 2005, Sandvik *et al.* 2012). This has been documented across various seabird species and populations, but the extent of the effects may vary between different taxa (Sandvik *et al.* 2012). This knowledge of species demography and environmental change is important to understand fluctuations in bird populations (Sæther *et al.* 2000).

Of the predicted effects of climate change, the dominant consequence is increased air temperature at the ocean and land surface (Oswald and Arnold 2012). Other variables of climate change that affect bird populations are: increases in the mean annual temperature, the mean annual minimum and maximum temperatures, with the annual minimum temperature exerting a larger influence, changes in the land surface precipitation and an increased frequency of extreme weather events (Lemoine 2005). Extreme weather events, such as storms and the increased frequency of these events, have a devastating effect on bird populations (Crick 2004). The causes underlying population trends can be determined by comparing population trends and the external variables can be used to help indicate the cause (Green 1999). It is important to distinguish between short-term and long-term trends that result from climate change, because marine ecosystems are dynamic and in a constant state of change (Crawford and Altwegg 2009). In this study I examined the bank cormorant population over a 56-year period.

The bank cormorant is an endemic, 'endangered' marine bird species that occur along the western coast of southern Africa. The bird has suffered a serious decline in its overall population, declining from c. 9000 breeding pairs between 1975 and 1981 (Cooper 1981) to approximately 3000 breeding pairs in 2011 (Crawford *et al.* 2012).

Crawford *et al.* (2008) considered that climate change had influenced the observed range shifts and population decreases of the bank cormorant, through the impact of climate change on the bank

cormorant's main prey species. The northern most bank cormorant colony in the Western Cape at Lambert's Bay, became extinct in 1999, which coincides with large decreases at the Dassen and Malgas Island colonies during the 1990s. Available evidence suggested that predicted climatic warming can raise environmental temperatures beyond that tolerable to seabirds (Oswald and Arnold 2012).

Many aspects of the life-histories of seabirds respond to climatic conditions (Sandvik *et al.* 2005), and it has been shown that climate variables can effect population dynamics through traits such as productivity (reproductive ability) and adult survival (Jenouvrier *et al.* 2005b). Population dynamics is a function of all life-history traits, and this may result in climate change operating at different time lags on a bird's population (Jenouvrier *et al.* 2005a, Sandvik *et al.* 2012). The impact of time lags in the life history of seabird populations may be important in explaining the fluctuations in population dynamics (Jenouvrier *et al.* 2005). It is important to understand whether the environmental influences the population growth via adult survival or a delayed reaction via offspring reproduction and recruitment (Sandvik *et al.* 2012). Recruitment, a demographic parameter is expected to have a delayed effect on population size and adult survival is expected to have an immediate effect (Jenouvrier *et al.* 2005a). Due to age of maturity (seabirds are long-lived), the effect of climate variation at one time may only be observed several years later (Durant *et al.* 2004). Bank cormorants generally reach maturity after three years and are then recruited into the adult population (Crawford *et al.* 2001). The detection of the negative effect of climate change on seabirds, is expected to be more likely when time lags of this length are included in the analysis.

Understanding how seabird populations respond to past climate change can help us comprehend their response to predicted future climate change (Bolger *et al.* 2005) and estimation of demography changes for bird populations is important in determining the conservation goal for that population (Green 1999). It is important to understand this response of seabird to climate change as seabirds may be used as early indicators of climate change. Furthermore, the conservation status of birds can be altered by climate change, resulting in changes in the conservation management of a community or species (Crawford and Altwegg 2009).

The aim of this chapter was to determine the long term, direct effects of climate change on an endangered species' demography, the bank cormorant. Long-term studies provide insight into how changes in the physical environment may affect seabird populations (Jenouvrier *et al.* 2003). The population of the bank cormorant has decreased to approximately 3 000 breeding pairs in 2011 (Crawford *et al.* 2012). Restricted range species, such as the bank cormorant which breed mainly on offshore islands, are more likely to be threatened by extinction than other species (Simmons *et al.* 2004). It was predicted that the decrease in the bank cormorant population is a consequence of a rise in atmospheric temperature, a decrease in rainfall and an increase in storms. Evidence shows that

the bank cormorant population has changed with fewer birds colonising fewer locations today, compared its historical population (Crawford *et al.* 2008).

## 4.2 Material and Methods

### 4.2.1 Study sites

The population data (1956–2012) analysed in this chapter were collected as part of a long-term bank cormorant population monitoring programme by the South African Government (Branch Oceans and Coasts, Department of Environmental Affairs) (Makhado *et al.* 2013). The colonies at which data were collected ranged from Lambert's Bay (Bird Island; 32°05' S, 18°18' E), the northern most colony, to Dyer Island (34°34' S, 19°21' E), in the south-east (Figure 4.1).

Bank cormorants nests were counted visually during the breeding season, with the highest count in a year taken to represent the number breeding at a colony (Crawford *et al.* 1999). The census of breeding bank cormorants started in 1956 for Lambert's Bay, Malgas Island (33°02' S, 17°55' E), Marcus Island (33°14' S, 17°58' E), Jutten Island (33°04' S, 17°57' E), Vondeling Island (39°09' S, 17°58' E) and Dyer Island. The first counts Robben Island (33°48' S, 18°21' E) and Dassen Island (33°25' S, 18°04' E) were in 1978. Counts were made infrequently until 1990 and then more regularly (Green 1999). Breeding bank cormorants were first observed at Stony Point in 1987 (Cooper 1988). Stony Point (34°22' S, 18°53' E) counts were provided by Bruce Dyer (Branch Oceans and Coasts, Department of Environmental Affairs 2013) and began in 1996.

### 4.2.2 Climate variables

Two climate variables, mean maximum temperature (°C) and total rainfall (mm) were used to determine the potential impact of climate change on the bank cormorant population in the Western Cape. Climate data used in this study were provided by the South African Weather Service (SAWS). Weather stations located at Cape Town (33°58' S, 18°36' E), Hermanus (34°25' S, 19°34' E) and Langebaan (32°58' S, 18°09' E) were chosen. Calculated yearly mean maximum temperature and yearly total rainfall were compared to long-term bank cormorant population data. The Lambert's Bay colony was not compared to weather data because the colony went extinct in 1999. The weather stations were chosen because they were closest to the above mentioned monitored colonies.

### 4.2.3 Statistical analyses

Not all colonies were counted every year. Missing observations were imputed, so that the total population sizes for each year, including those years with a few missing observations, could be estimated. The method devised by Underhill and Prys-Jones (1994) was used. They stated that imputing the missing values could be done providing there was a suitable statistical model. This is the same model used by Underhill and Prys-Jones (1994) for waders in the United Kingdom. The

imputed values should be a small part of the total number of counts (Underhill and Prys-Jones 1994). Imputation was done using Fortran (Fortran Working Group). Imputed data provided a complete data set for the bank cormorant population at each colony.

Linear regression models and correlation statistics were used to determine if relationships existed between the population dynamics and climate variables. Statistical modelling of the relationship between climatic parameters and species populations is now a widely accepted method for studying climate-species interactions (Kearny 2011). Time lag analysis, important in determining population dynamics (Jenouvrier *et al.* 2005a, Thompson and Ollason 2001), was also applied. Bank cormorants only become part of a breeding population at three years of age. The same climate variables were analysed with the population index with a time lag of three years using the software package R v.3.0.3 (R Development Core Team 2009). This way fecundity (reproductive effort) as a life-history trait is analysed in relation to climate change.

## **4.3 Results**

### **4.3.1 Population size**

The overall pattern for the number of bank cormorants breeding at nine well-monitored localities in the Western Cape in the six-decade study period from the late 1950s to the early 1990s was decreasing, although there were large fluctuations (Table 4.1 and Figure 4.2). The populations at the individual colonies showed strong year to year variation (Table 4.1). Bank cormorant populations at Vondeling, Juttten, Dyer and Malgas Islands decreased from the late 1990s to the early 2000s. Lambert's Bay's population decreased from the early 1990s to complete abandonment in 1999. Marcus Island's colony was relatively stable in size and the Robben Island population showed a slow increase since monitoring began. At Stony Point, a colony was initiated in 1987, and subsequently, increased.

To determine the population index of the bank cormorant, imputed values were used (Table 4.1). I set the population size index to 100% in 1956, when the estimated population size for the nine breeding bank cormorant colonies used in this study was 763 breeding pairs. This resulted in 35 imputed values. In relation to this baseline the population size index for the bank cormorant population in 2012 was 34.45% (Figure 4.2). This showed a decrease of 65.5% in the 56 years leading up to 2012. The total population of all the colonies in 2012 was the lowest it's been since 1956.

The Lambert's Bay bank cormorant colony (Figure 4.3a) decreased to local extinction in 1999. By 2012 this colony had not re-established itself. Like Lambert's Bay, Malgas Island (Figure 4.3b) showed a decrease in the bank cormorant colony, to only nine breeding pairs in 2012. This represented a decline of 91.2% since 1956. From 1990 to 1995, the population declined by 71.1% from 194 to 56 breeding pairs.

Marcus Island on the West Coast was relatively stable during the study period, with only small annual fluctuations (Figure 4.3c). However, the colony showed a small increase of 10.7% from 1985–2012.

The bank cormorant colony at Vondeling Island (Figure 4.3d) decreased from 1956–1986 and increased again up until 1994. From 1994 to 2012 the breeding colony decreased from 65 to 3 breeding pairs, representing a decline of 95.4%. The total population decline from 1956–2012 is c. 90%. The Jutten Island colony (Figure 4.3e) also showed an overall decrease from 1956–2012, but with clear annual fluctuations. The colony decreased from 40 breeding pairs in 1956 to 19 pairs in 2012 (52.5% decrease).

Although there has been a total decrease of 73.56% since 1956, Dassen Island (Figure 4.3f) is one of the few bank cormorant colonies that showed an increase in breeding pairs from 1995–2012. The colony has increased from 25 pairs to 70 pairs between 1997 and 2012. That is an increase of more than 100% for that time period. The bank cormorant colony at Robben Island (Figure 4.3g) has been relatively stable in the 56 study years (1956–2012), with some annual fluctuations and an increase of just over 20% until 2011.

For the Stony Point data set (Figure 4.3h), the newest of the bank cormorant colonies in the Western Cape, counts started in 1987 with two breeding bank cormorant pairs (Table 4.1). This increased to 32 breeding pairs in 2012.

The bank cormorant colony at Dyer Island (Figure 4.3i) decreased by 94% from 1956 to 2012. A period of decrease for this colony occurred between 1997 and 2012, during which breeding pairs decreased by almost 90%.

#### 4.3.2 Population fluctuations and climate change

The Robben Island bank cormorant population, which presented an increase in population growth (Figure 4.3g) showed no significant correlation with changes in average maximum daily temperature ( $r_{26} = 0.047$ ,  $p > 0.05$ ) or total rainfall ( $r_{26} = -0.12$ ,  $p > 0.05$ ) over time, for the Cape Town weather station. However, the average maximum temperature in this region has shown an increase of 0.4 °C (0.02%) in the 35 years leading up to 2012 (Figure 4.4) ( $p = 0.0027$ ). Time lag analysis, with a period of three years (the time it takes for a bank cormorant to reach sexual maturity), did not reveal an effect of temperature ( $r_{23} = -0.022$ ,  $p > 0.05$ ) or rainfall ( $r_{23} = -0.089$ ,  $p > 0.05$ ) on the population dynamics of the bank cormorant.

The average maximum daily temperature per year for Hermanus showed no significant increase and the total rainfall per year showed only annual fluctuation. Temperature and rainfall were not correlated ( $r_{17} = 0.25$ ,  $p = > 0.05$ ). The increase in population growth at Stony Point (average maximum daily temperature:  $r_{18} = 0.10$ ,  $p > 0.05$ ; total rainfall:  $r_{17} = 0.0076$ ,  $p > 0.05$ ) was not related

to temperature or rainfall changes. Similarly the decrease at Dyer Island (average maximum daily temperature:  $r_{18} = -0.22$ ,  $p = 0.34$ ; total rainfall:  $r_{17} = -0.23$ ,  $p = 0.34$ ) was not related to temperature or rainfall change. With time lag analysis, neither of the two colonies displayed a relationship with rainfall (Stony Point:  $r_{14} = 0.032$ ,  $p > 0.05$ ; Dyer Island:  $r_{14} = -0.018$ ,  $p > 0.05$ ) or the mean temperature (Stony Point:  $r_{14} = 0.012$ ,  $p > 0.05$ ; Dyer Island:  $r_{14} = 0.40$ ,  $p > 0.05$ ).

Average maximum temperature at the Langebaan weather station (Figure 4.5) showed a significant increase of just over 0.06 °C (1%) ( $p = 0.009$ ) over time. The climate parameter total rainfall showed no trend over time ( $p = 0.71$ ). None of the bank cormorant colony populations around the Langebaan weather station (Malgas Island, Marcus Island, Jutten Island, Vondeling Island and Dassen Island) showed any relationship with either average maximum temperature or total rainfall (all  $p > 0.05$ ).

The time lag analysis produced significant negative correlations between the bank cormorant population for Malgas Island with average maximum daily temperature ( $r_{23} = -0.55$ ,  $p = 0.005$ ) (Figure 4.6). Similarly, Dassen Island had a negative correlation between the time lagged population and the temperature ( $r_{23} = -0.57$ ,  $p = 0.003$ ) (Figure 4.7).

#### **4.4 Discussion**

The imputed dataset was successful in helping with the analysis of the population data. It helped determine population trends of bank cormorant colonies in the Western Cape, South Africa.

This study showed that the South African bank cormorant population has decreased considerably from 1956 to 2012, with some colonies going extinct. This decrease presents a more than 30% decline over 50 years leading up to 2012. The changes in population size are the result of various factors, which may operate, as seen in this study, independently over different time scales (Jenouvrier *et al.* 2003).

Inter-annual variation is clear for all the bank cormorant colonies. Inter-annual variability is a well-recognised occurrence in marine ecosystems with fluctuations in environmental parameters affecting all trophic levels (Jenouvrier *et al.* 2005a). These fluctuations affected by environmental variability can affect the survival of a species (Jenouvrier *et al.* 2005b). Environmental parameters may affect the ease of access and availability of needed resources which might affect the survival and productivity of a species (Jenouvrier *et al.* 2003).

All colonies showed a large decrease in breeding pair numbers in the early 1990s. This can also be seen in the combined population index of the studied bank cormorant colonies between 1989 and 1995.

The colony at Lambert's Bay never recovered from the population decrease and went extinct in 1999. This decrease does not seem to be related to climate variability, but rather to a food resource shortage.

Crawford *et al.* (2008) stated that the bank cormorant numbers breeding at Lambert's bay were significantly related to rock lobster *Jasus lalandii* landings in fishing zones near the colony. The extinction of the colony can also partly be attributed to the displacement of birds from their breeding location by Cape fur seals *Arctocephalus pusillus pusillus* (Crawford *et al.* 1999).

The bank cormorant colonies at Malgas, Vondeling and Jutten Islands all showed large decreases in the early 1990s. Since the mid-1990s, Malgas Island's population decrease slowed down, but both the colonies at Vondeling and Jutten Islands still showed a decrease in 2012. The decreases in the sizes of the colonies on Malgas, Vondeling and Jutten Islands did not show any relationship with an increase in mean annual temperature or a decrease in total annual rainfall. However, the size of the colony at Malgas Island showed a negative correlation between the lagged effects of temperature increase and the population trend.

This suggests that increased temperatures could affect the reproductive success of the bank cormorant colony, leading to a decrease in the population due to less adults being recruited into the breeding population. Sherley *et al.* (2012) showed that extreme temperature events killed bank cormorant chicks in nests at Mercury Island, Namibia. Crawford *et al.* (1991) stated that the adult survival of bank cormorants is expected to be about 80%. This further suggests poor recruitment to be the reason for the population decline at Malgas Island (Crawford *et al.* 2008). Jenouvrier *et al.* (2005a) also suggested that environmental factors influencing the recruitment of seabirds into the breeding population may affect the population size.

The decrease in the sizes of the colonies at Jutten Island and Vondeling Island could be attributed to the large reduction in the growth rate of rock lobster *Jasus lalandii* from 1985 to 1991 (Cruywagen 1997). The smaller size of rock lobsters may not be able to offer enough food resources to support large colonies on these islands (Crawford *et al.* 2008a). The populations at both these islands seem to fluctuate quite regularly. An increase in population will most likely be due to immigration by first-time breeders (Crawford *et al.* 2008a) but this seems to always be followed by an even larger decrease resulting in an overall population decrease since the late 1980 and early 1990s.

Like the rest of the West Coast colonies, the colony at Marcus Island showed a decrease in the breeding population in the early 1990s. However, the number of breeding pairs was relatively stable from 2003 to 2012, even displaying a slight increase after 2008 until 2012. Marcus Island therefore seems not to be currently affected by climate change or a lack of food resources. With these results, Crawford *et al.* (2008)'s conclusion is further supported, that it appears that bank cormorant offshore islands in the Saldanha Bay on the West Coast, seem to be able to support small bank cormorant breeding populations, even when this study suggests evidence for increased mean daily temperatures.



The colony at Dassen Island had a large decline in its breeding population from 1989 to 1990 with a smaller decline up until 1994, but increased again from 1994–2012. Dassen Island's bank cormorant colony did not show any correlation with changes in mean annual temperature or total annual rainfall with the population numbers. The Dassen Island population did however show a negative correlation with the lagged effect of an increase mean annual temperature on reproductive success, suggesting that temperature change might be responsible for changes in the Dassen Island colony. However, Crawford *et al.* (2008) also explained that the decrease in bank cormorant colony in the early 1990s was related to a decline in the rock lobster population.

The breeding bank cormorant population at Robben Island showed large annual fluctuations. Overall the colony increased since 1978 when 64 breeding pairs increased to a maximum of 148 breeding pairs in 2011. The colony has steadily increased since 2002, with the exception of 2012. No relationship exists between colony numbers and changes in annual temperature and rainfall (not for direct effect or time lag analysis), suggesting that a different environmental parameter is responsible for the increase in the cormorant population at Robben Island. The waters around Robben Island were declared a rock lobster reserve in 1960 (Pollock 1997), resulting in no legal commercial fisheries extracting the bank cormorant's food resource around the island.

Breeding bank cormorant numbers at Stony Point have increased since the foundation of the colony in 1987 (Cooper 1988). Data show that the Stony Point colony has increase by more than 350% from 1996–2012. Bank cormorant population growth here was not correlated with an increase in annual mean temperature or annual rainfall for adult survival or reproduction productivity. The bank cormorant population here is likely not limited by food resources (Crawford *et al.* 2008a) and is permanently protected from disturbance by humans and most predators (Cooper 1988), therefore an exponential increase is not surprising. Stony Point has been colonised in spite of higher temperatures and lower rainfall.

Dyer Island's bank cormorant population showed an overall decline of 94% from 1956 to 2012, with the largest decline occurring between the late 1990s and 2012. Results indicate that this decrease in breeding numbers is not connected to a change temperature or a rainfall, but the relationship between the population size is correlated with time lagged analysis of the climate parameters. This again suggests that climatic events impact the breeding populations rather through an influence on fecundity than directly on the adult survival of the species.

Overall the direct impact of climate change on adult survival of the bank cormorant showed no significance in the bank cormorant population at either one of the colonies. Neither increased annual mean temperature nor decreased total rainfall had a direct effect on a population count of a similar year, even though there was a definite increase in mean annual temperature in Cape Town (Robben Island) and all the West Coast colonies.

If the climate effect is most pronounced at a time lag effect of three years, it can be that offspring production is the fitness component that responds most to climatic variability, as found by Sandvik *et al.* (2012). However, unlike this study, Sandvik *et al.* (2012) found that both adult survival and offspring reproduction are affected by climate change, but the effect is more pronounced for offspring reproduction and recruitment.

When a time lag of three years was implemented (to include the delayed effect of recruitment), the colonies that seemed to produce evidence for a relationship with an increase in temperature were the colonies at Malgas and Dassen Islands. Both these colonies have suffered a significant decrease in their populations since 1956. Malgas Island which supported more than 150 breeding pairs in the 1990s, had only nine breeding pairs left in 2012. Delord *et al.* (2004) suggested that the breeding success of a species in one year may affect the number of breeders in years to come. This provides evidence that if these colonies are affected by climate change, but only with a time lag of three years, the climate changes might affect the reproductive output of that year, and therefore the size of the population three years later. On a study of northern fulmars *Fulmarus glacialis*, it was similarly found that among long-lived species, like the bank cormorant, environmental variability influences reproductive success, and therefore climate change effects are likely to be lagged, influencing population numbers at later years when new birds are recruited into the breeding population (Thompson and Ollason 2001).

The colony at Dassen Island displays an overall decrease in breeding population of almost 74% from 1956 to 2012, but has shown an increase in the last 15 years of that period, in spite of a temperature increase. This goes against the assumption that the decrease in the population at Dassen Island is related to an increase in mean annual temperature.

#### **4.5 Conclusions**

This study provides evidence that there is a decrease in the bank cormorant population in the Western Cape. However, this decrease is less related to climate change in this region, than previously stated in the hypothesis, even though the IPCC (2013) reports that the 2000s is the warmest decade yet. The effects of climate change on the decreasing population through adult survival was non-existent and the lagged effects of climate change on breeding numbers was apparent for some colonies, but not for others.

According to the life-history theory, adult survival is the most important variable life-history parameter for long-lived seabird, and is therefore expected to be the life-history trait that will be least affected by climate variability and change (Jenouvrier *et al.* 2005a). A decrease in adult survival should have an immediate effect on a breeding population, but a decrease in fecundity will only have a delayed effect as displayed by the lagged effect (Jenouvrier *et al.* 2005a). The unwillingness of

seabirds to risk their own survival might explain why population size changes act through seabird recruitment rather than adult survival (Jenouvrier *et al.* 2005a) and why time lag analysis produce better results than analysis of the effect of climate change directly on the adult population.

However, given the length of time series to date, we cannot exclude some of these changes with certainty as not related to anthropogenic global warming. As none of the life-history traits of seabirds can be excluded in determining the cause of population decline, I conclude that fluctuations in the breeding population reflect interactions between the climate variability and the trade-off between adult survival and reproductive effort, affected by various environmental parameters. To further investigate this, I suggest determining long-term trends in breeding success of the bank cormorant in relation to climate change.

Table 4.1. Bank cormorant breeding pair counts for nine colonies in South Africa in 1956, 1977–1980 and 1985–2012. Bold counts represent imputed values

Year	Lambert's Bay	Malgas Island	Marcus Island	Vondeling Island	Jutten Island	Dassen Island	Robben Island	Stony Point	Dyer Island	Total	Population index
1956	69	102	43	29	40	<b>265</b>	<b>115</b>	0	100	763	100
1977	<b>49</b>	146	20	<b>25</b>	53	<b>242</b>	<b>106</b>	0	<b>57</b>	698	91.48
1978	6	85	26	28	30	211	64	0	20	470	61.57
1979	36	121	19	1	24	118	73	0	14	406	53.19
1980	33	110	23	<b>17</b>	23	121	59	0	35	421	55.09
1985	<b>33</b>	106	28	17	39	130	97	0	37	487	63.83
1986	<b>25</b>	<b>92</b>	<b>22</b>	<b>25</b>	47	<b>135</b>	83	0	7	436	57.02
1987	<b>29</b>	79	24	46	35	219	89	2	<b>28</b>	551	72.21
1988	18	<b>115</b>	<b>22</b>	<b>31</b>	<b>37</b>	132	108	<b>2</b>	<b>25</b>	490	64.22
1989	33	164	<b>31</b>	<b>47</b>	35	204	107	<b>3</b>	<b>37</b>	661	86.63
1990	23	194	24	25	52	107	134	<b>3</b>	44	606	79.42
1991	16	119	34	57	58	131	132	<b>4</b>	27	578	75.75
1992	13	125	18	42	61	90	111	<b>5</b>	15	480	62.90
1993	11	101	22	33	54	70	115	<b>5</b>	<b>21</b>	432	56.61
1994	11	72	23	65	52	16	100	<b>6</b>	23	368	48.23
1995	4	56	21	40	45	36	73	<b>6</b>	17	298	39.07
1996	2	30	25	44	42	31	89	7	45	322	41.27
1997	1	32	34	31	47	25	106	22	57	355	46.51
1998	1	28	27	20	49	29	79	<b>13</b>	57	303	39.66
1999	0	23	27	24	61	46	101	14	38	334	43.76
2000	0	24	27	36	61	41	120	15	49	373	48.87
2001	0	29	29	27	43	54	68	13	47	310	40.61
2002	0	28	17	42	40	51	65	<b>13</b>	36	292	38.27
2003	0	24	24	17	34	50	85	13	33	280	36.68
2004	0	21	27	26	50	47	99	17	38	325	42.58
2005	0	17	24	24	41	52	113	22	30	323	42.32
2006	0	9	27	17	30	30	136	26	26	301	39.43
2007	0	4	27	14	24	55	121	24	22	291	38.12
2008	0	11	27	19	29	66	118	37	13	320	41.92
2009	0	11	32	5	16	56	135	41	6	302	39.56
2010	0	9	30	6	27	42	114	28	9	265	34.72
2011	0	8	30	3	24	81	148	31	9	334	43.76
2012	0	9	31	3	19	70	93	32	6	263	34.45



Figure 4.1. Location of the bank cormorant colonies in the Western Cape, South Africa

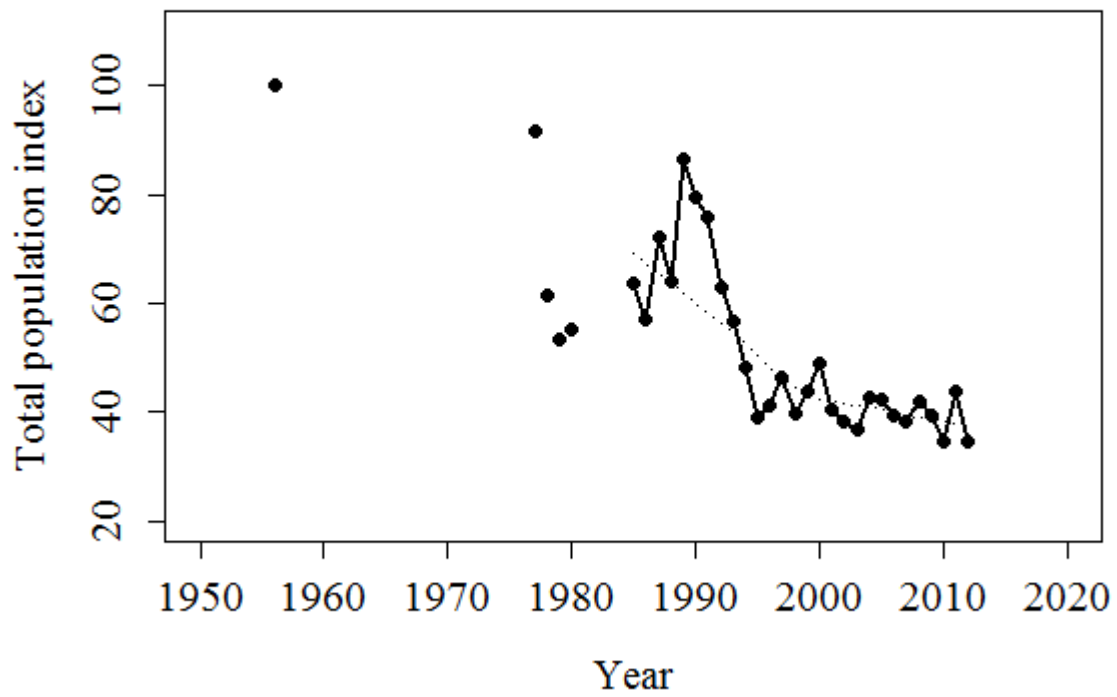


Figure 4.2. Population index with regression since 1985 (dashed line) for nine bank cormorant colonies in the Western Cape, South Africa

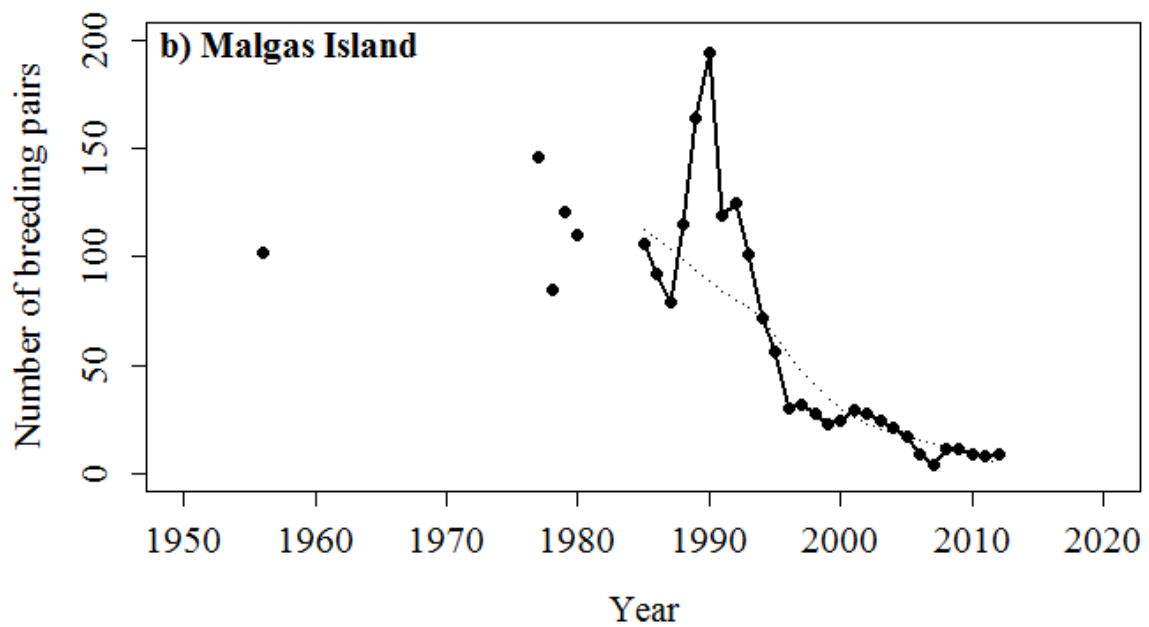
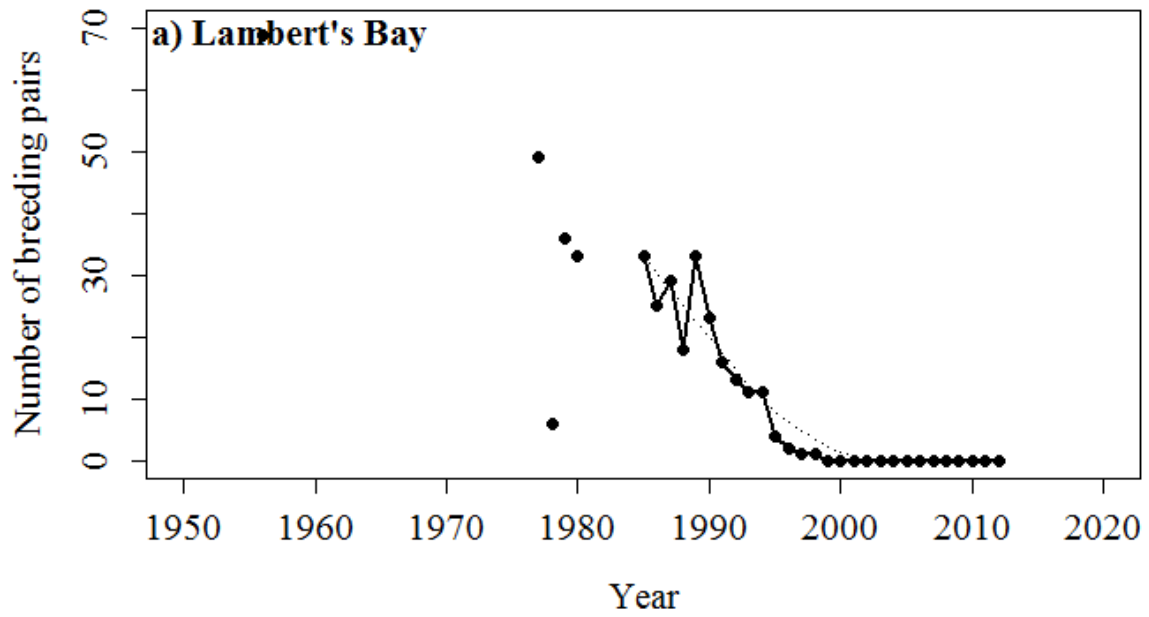


Figure 4.3. The annual variation of the number of bank cormorant breeding pairs with regression since 1985 (dashed line) at nine Western Cape colonies during 1956–2012: a) Lambert’s Bay, b) Malgas Island, c) Marcus Island, d) Vondeling Island, e) Jutten Island, f) Dassen Island, g) Robben Island, h) Stony Point and i) Dyer Island

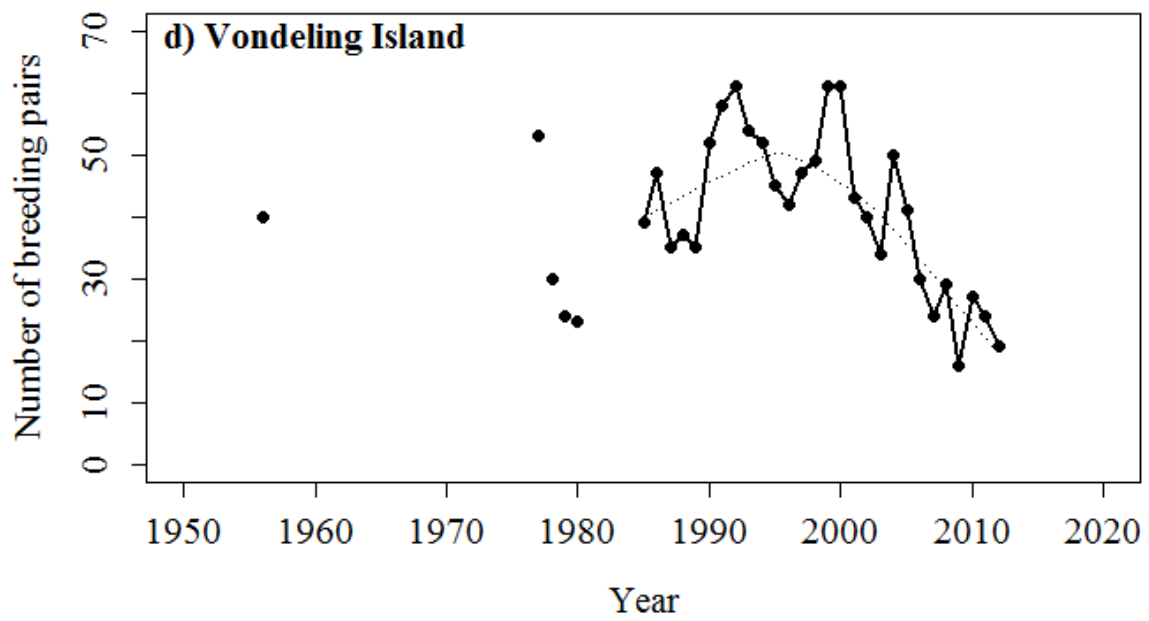
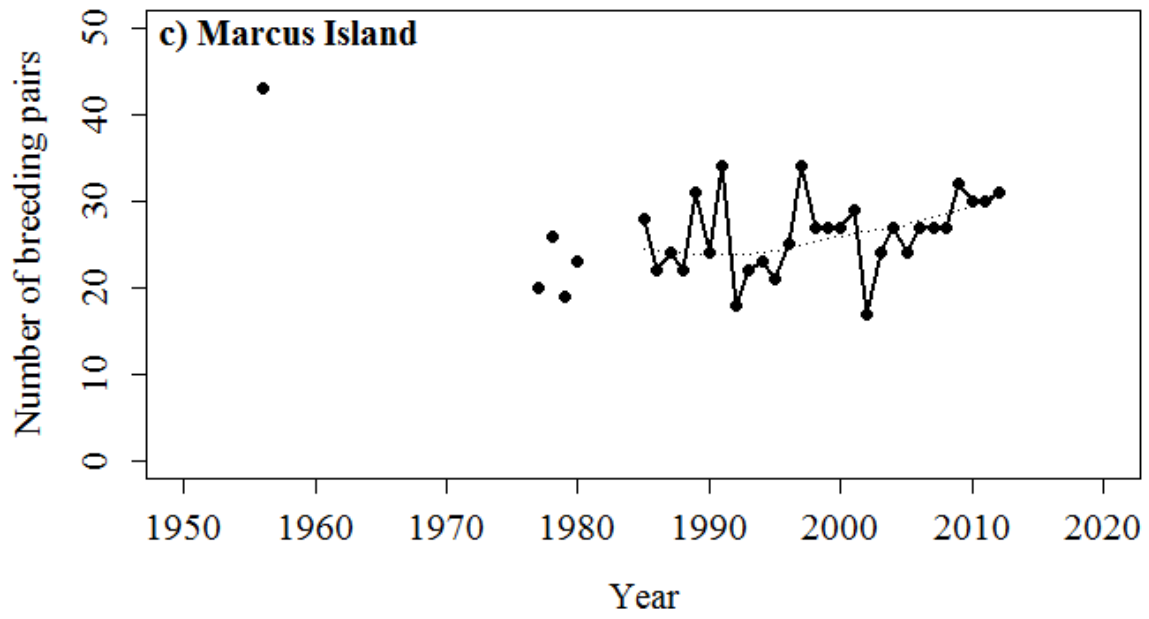


Figure 4.3 continued



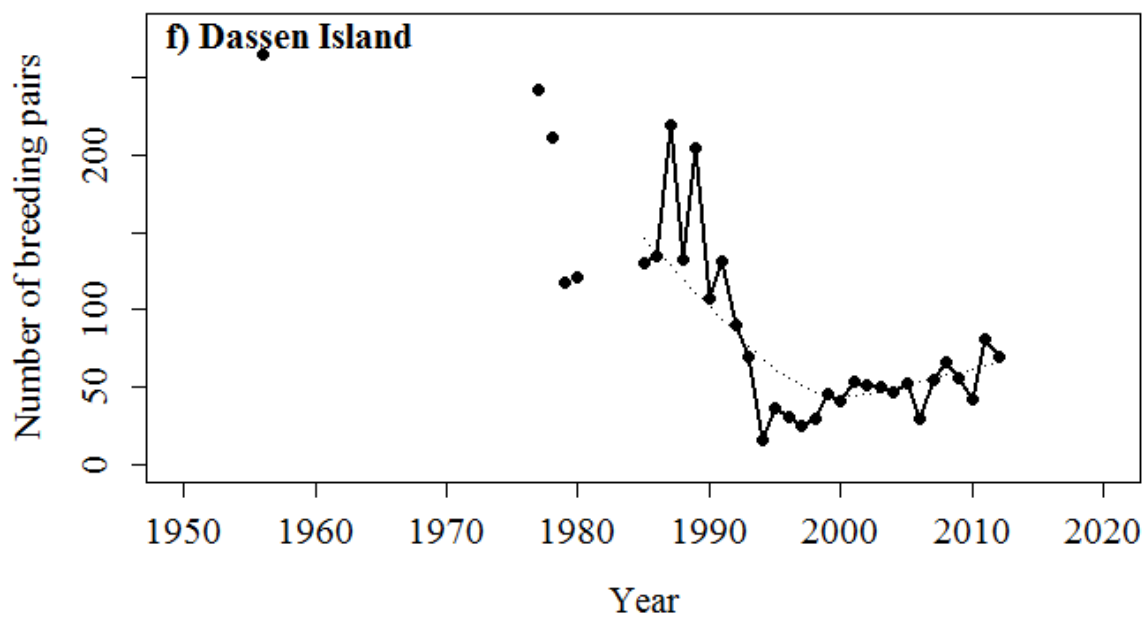
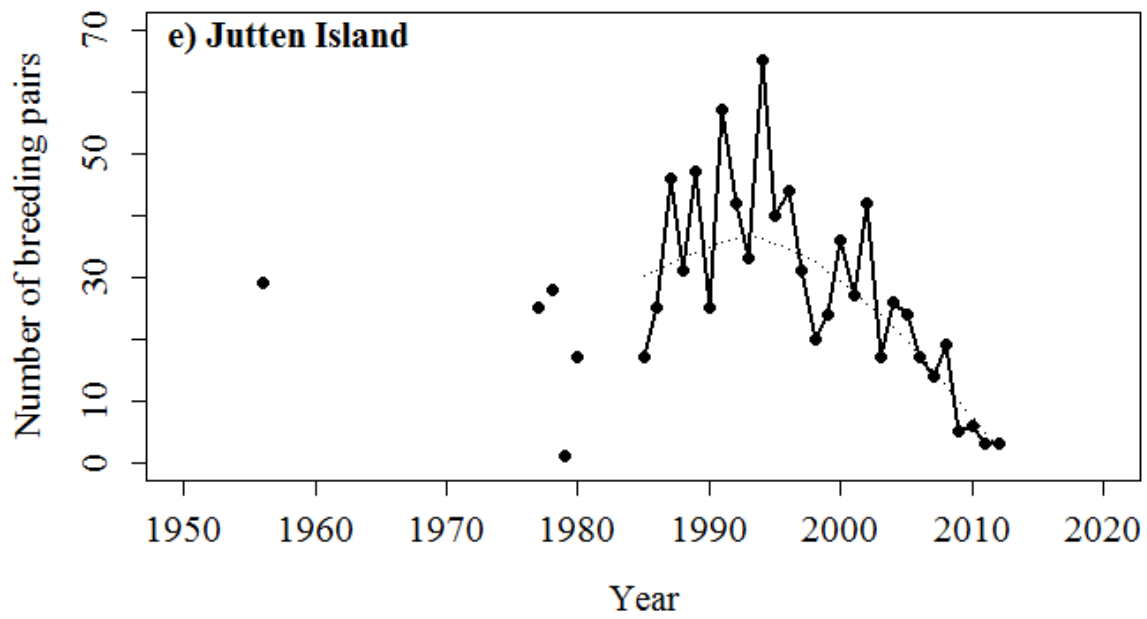


Figure 4.3 continued

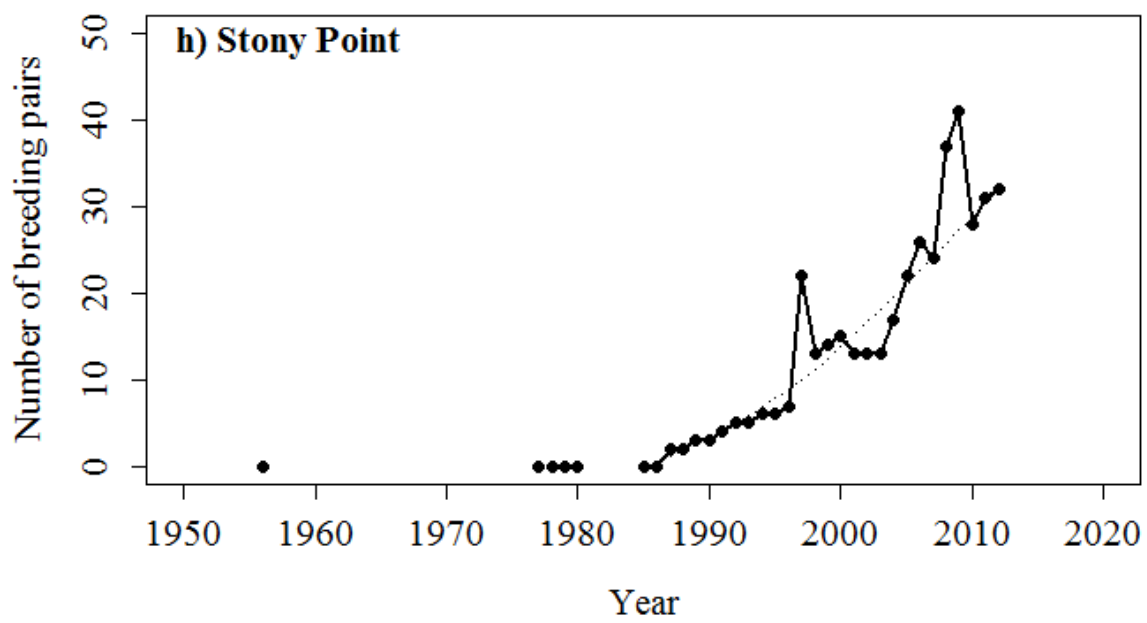
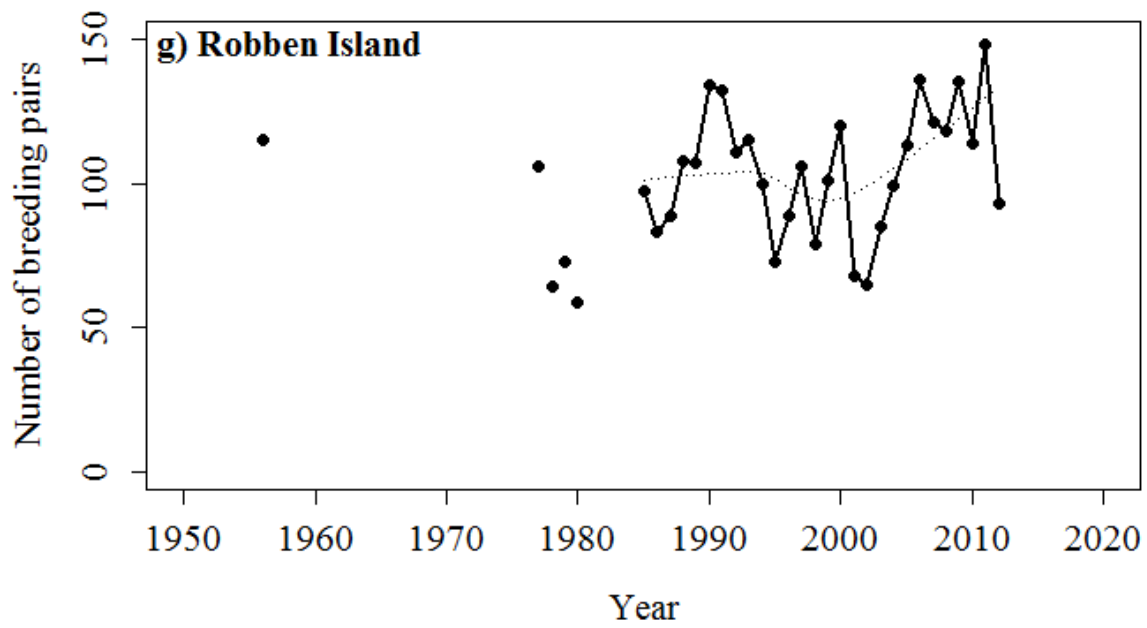


Figure 4.3 continued

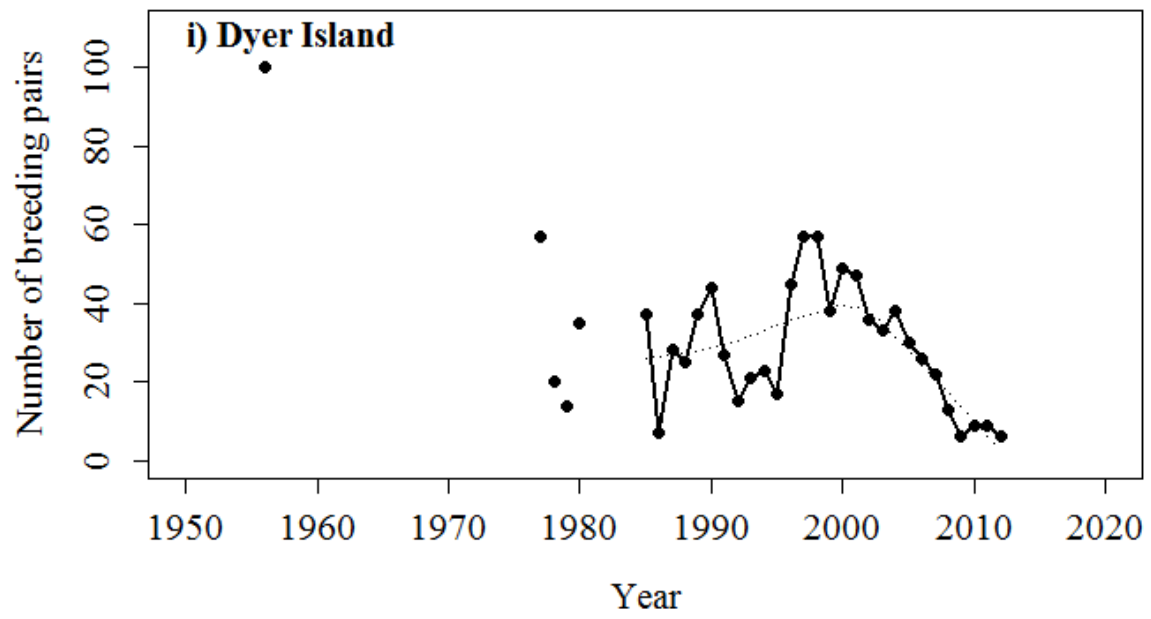


Figure 4.3 continued

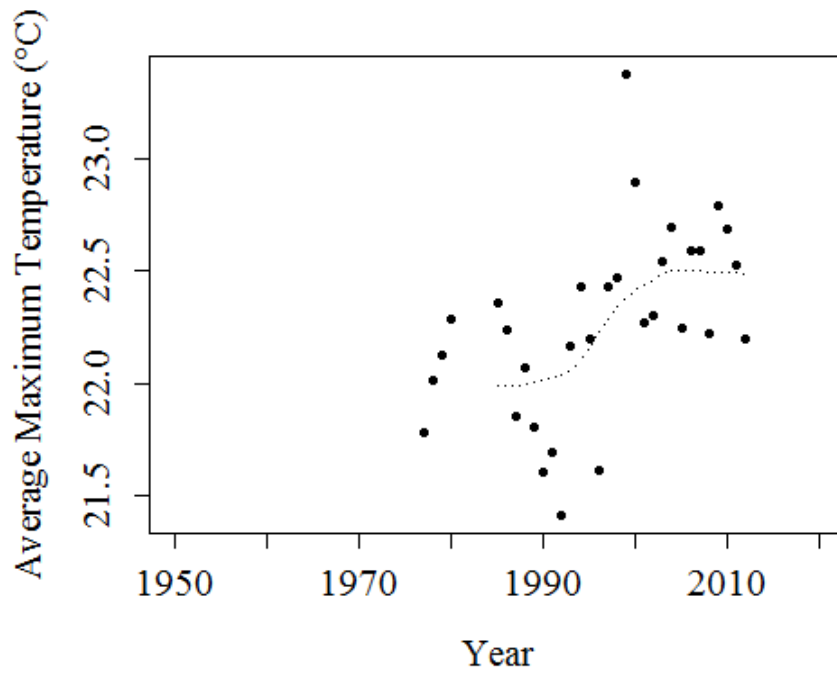


Figure 4.4. Average maximum temperature at Cape Town, 1977–2012

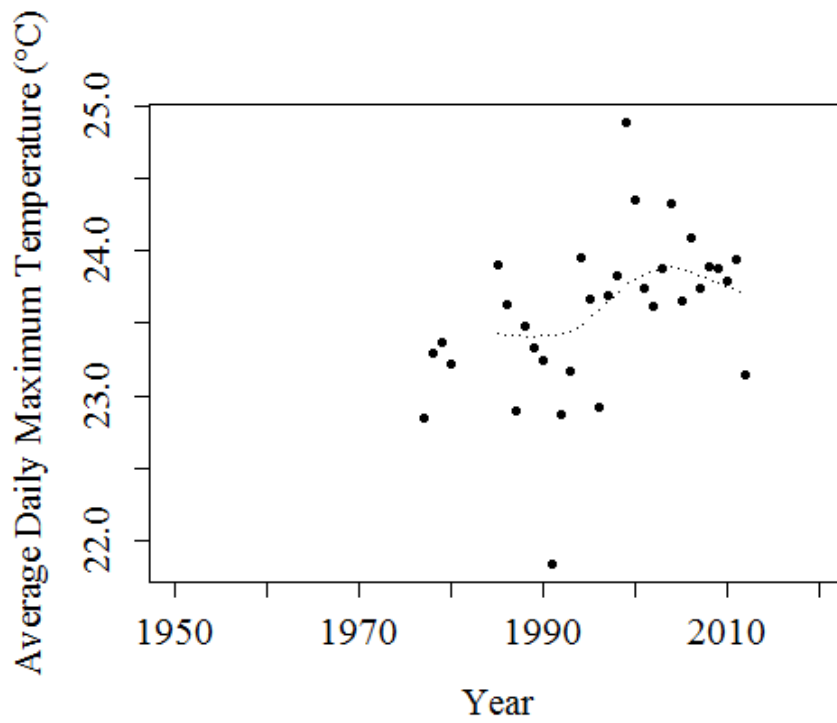


Figure 4.5. Average maximum temperature at Langebaan, 1975–2012

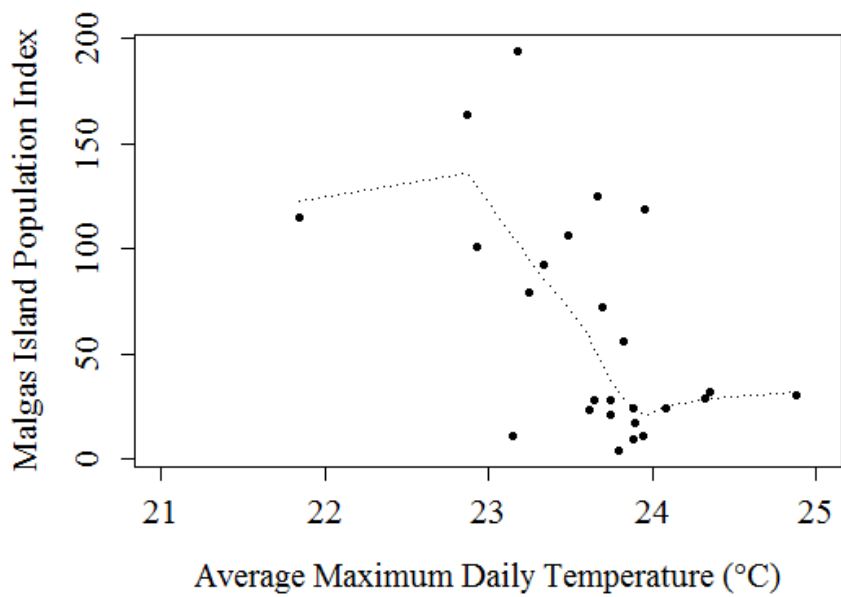


Figure 4.6. Relationship between average maximum daily temperature (°C) as a time lag and the Malgas Island population index

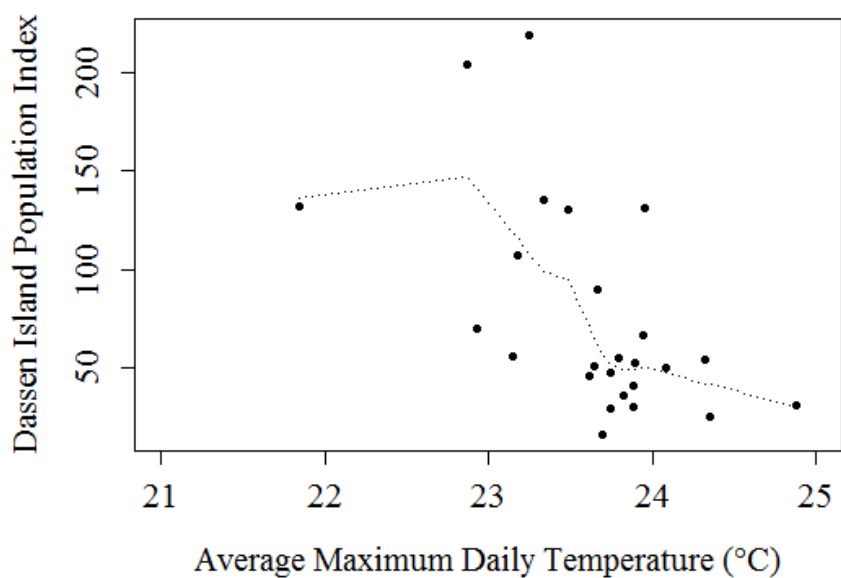


Figure 4.7. Relationship between average maximum daily temperature (°C) as a time lag and the Dassen Island population index

## Summary and conclusions

It is clear that the bank cormorant's population is declining, and that many bank cormorant colonies in the Western Cape are under threat of extinction. The colony at Lambert's Bay (Bird Island) has locally extinct since 1999. Populations at Dyer, Vondeling, Malgas and Jutten Islands were still declining at the end of this study in 2013, while the populations at Robben, Dassen and Marcus Islands and Stony Point seem to be increasing in numbers. In South Africa, not all smaller bank cormorant colonies are in protected areas and human access can be easily gained (du Toit *et al.* 2002). Therefore it is of great importance for conservation management to realize that the larger portion of the bank cormorant population is concentrated at only a few colonies and to prevent further decline of the population by securing these colonies.

Most previous studies focused on the indirect effect of climate change on seabird populations, rather than the direct effects (Oswald and Arnold 2012). There are clear indications that climate change is occurring and will continue to accelerate in the future, and that it has direct and indirect effects on seabirds (IPCC 2007). Climate change in itself can be difficult to model and predict and even more difficult to manage (Young *et al.* 2012). This research aimed to identify the impact of direct climatic variability on the population and breeding parameters of the bank cormorant. To summarise, the research found evidence that the population dynamics of bank cormorants is affected by climatic variability on nest survival, but likely not through direct impacts of climate change on adult mortality, resulting in direct population decline. The patterns we observed can lead to several predictions on how climate change might affect the population of the bank cormorant in the future.

Under the current climatic conditions, the breeding bank cormorant seems to be able to adequately thermoregulate during periods of high or extreme temperatures. During the filming analysis, no birds actively sitting on a nest were observed leaving the nest when experiencing high heat loads. These current observations are further supported by the result that failures during the breeding period did not seem to be affected by increasing mean maximum temperatures.

The relationship between bank cormorant breeding success and environmental variables has been documented in this study and it does suggest that there are certain climatic variables that influence the breeding success of the bank cormorant. Understanding this relationship is vital for the survival of this species. These include increased wind speeds and increased wave heights and both seem to be related to storm events. The relationship between increased wind speed and bigger wave action and breeding success suggest that the frequency of these events could have detrimental effects on the future reproductive output of this species. Extreme events, like storms, are predicted to become more frequent with future climate changes and this increased climatic variability is expected to affect not only the bank cormorant's breeding success, but most marine ecosystems (Frederiksen *et al.* 2008).

Climate change impacts processes related to fecundity and survival (Watkinson *et al.* 2004). It is assumed that, where breeding habitats of seabirds are not disturbed by anthropogenic activities or environmental variability, bird populations will remain relatively stable over a long period (Micol and Jouventin 2001). Bank cormorants, however, are very susceptible to human disturbance. At colonies where anthropogenic activity is high, the breeding site might be confined to a small space, more exposed to weather elements and restricted to lower lying areas closer to the water. Management efforts should therefore focus on limiting human disturbance and development at breeding locations (du Toit *et al.* 2002) and expanding breeding locations with artificial structures because the bank cormorant colony, at Robben Island, breeding on manmade breakwaters is relatively stable (Sherley *et al.* 2012).

However, where changes in nesting success and mortality occur during the breeding season, it can be difficult to distinguish if they result from the impact of climate or the impact of fishing (Duffy and Schneider 1994). This is a shortcoming in this study, and I suggest further research in combining the impact of these two variables on the breeding success of the cormorant. Researchers need to understand the effect of both changes in the physical environment and food resources at different stages of a seabird's lifecycle in order to predict long-term consequences of this change (Croxall *et al.* 2002). Oswald and Arnold (2012) suggest that detailed studies of the breeding success and adult survival that examine the importance of thermal stress on a species should also incorporate the indirect climate effects. This integration of effects will enhance our abilities to pinpoint all the variables responsible for the decline of the bank cormorant and help us understand the changes of other seabird populations as a result of variable climate.

Climate change will most likely make weather variables an increasingly important factor in the reproduction effort of seabirds (Boersma and Rebstock 2014) and to conclude, it seems like a long-term monitoring programme is needed to better understand the impact of environmental variables on the population dynamics and breeding success of the bank cormorant population in the Western Cape, South Africa.

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