Effects of temperature on gular fluttering and evaporative water loss in four sympatric cormorants in southern Africa

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February 17, 2014

Submitted in partial fulfilment of the requirements for the degree of

Masters of Science in Conservation Biology by coursework and dissertation

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PLAGIARISM DECLARATION

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

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ABSTRACT

Climate change continues to cause rising air and sea surface temperatures and changes in precipitation patterns across the globe. Many seabirds will be challenged by increasing temperatures because they must balance conflicting adaptations for dealing with cold environments when foraging and hot environments when nesting. Heat stressed seabirds often gular flutter for thermoregulation, a behaviour that is effective for dissipating heat but expensive in terms of evaporative water loss. This study examined gular fluttering behaviour of four species of southern African cormorants, crowned (*Microcarbo coronatus*), Cape (*Phalacrocorax capensis*), bank (*Phalacrocorax neglectus*), and white-breasted (*Phalacrocorax carbo luci*dus) cormorants. Results show that gular fluttering is influenced by temperature, body position and body size. Gular fluttering increases with temperature and larger cormorant species spend a greater proportion of time gular fluttering for a given temperature. Threshold temperatures for initiating gular fluttering are lower for large than for small cormorant species. Proportions of time spent gular fluttering are higher when birds are sitting than when crouching over the nest. Water loss shows the same pattern as gular fluttering, with the larger species estimated to lose a higher percentage of their daily water intake. Larger cormorant species can lose as much as 40% of their daily ingested water after eight hours of gular fluttering.

These findings indicate that temperature increases from climate change will likely have serious direct impacts on nesting cormorant colonies in southern Africa. Gular fluttering could increase by as much as 25% by 2100 under current projected temperature increases, and increases in water loss could reach nearly 10%. Some species may shift their breeding dates to compensate for increasing temperatures, but if breeding activities are timed to coincide with peaks in their main prey species, this may result in poorer diets or increased competition from other species.

ACKNOWLEDGMENTS

First of all, I want to thank the African Penguins on Robben Island. I wouldn't have visited Cape Town if they hadn't lured my partner Kate Robinson away from home to take up a PhD at UCT. I also want to thank Kate, and my family for the love and support they've given me while I'm away from home, my friends back in Canada for keeping me abreast of the goings on in the world of ice hockey (especially Hughie, John and Bruce), and my Cape Town friends who've made me feel at home.

Thanks also to my supervisors Tim, Richard and Peter for the stimulating discussions and guidance throughout the project. Thanks to Marc Burman for helping me understand how the moult model works. Thank you to the South African Weather Service for providing the Robben Island temperature data, and to Philna Botha, Corlia Meyer, and Emilee Sparks for collecting the temperature data at the colonies. Special mention to Jennifer Roberts for discussions about how to use Jwatcher and for providing me with all her Bank cormorant data to use in the thesis.

Finally, thanks to the CB class of 2013 for being so much fun and for sharing all the ups and downs of the past year. And finally, thanks to the cormorants. Just for being so cool.

INTRODUCTION

There is now strong scientific evidence that climate change has resulted in rising air and sea surface temperatures and changes in precipitation patterns across the globe (Trenberth *et al*. 2007). The globally averaged combined land and ocean surface temperature show a warming of 0.85°C from 1880 to 2012. This trend is likely to continue, with surface temperatures predicted for the end of the 21st century to be 1.5^{o}C higher than during 1850 to 1900 (IPCC 2013). In addition to rising temperatures, the frequency of storm and other extreme weather events have also increased throughout most of the world (IPCC 2013) and are projected to continue increasing.

In southern Africa, New *et al.* (2006) showed a general increase in the frequency of extreme hot days and nights and a decrease in cold extremes during the period from 1961 to 2000. Kruger and Sekele (2013) found similar trends from 1962 to 2009 and indicated that the western half of South Africa (as well as parts of the east) showed stronger increases in warm extremes and decreases in cold extremes than other parts of the country.

These changes will have significant impacts on biodiversity. Responses to climate change are already observable for many bird species, and include changes in phenology, distribution, demography, and individual behaviour (Walther *et al*. 2002, Parmesan 2006, Jenouvrier 2013). Models are now being used to predict future responses to climate change. Simmons *et al*. (2004) used bioclimatic niche models to predict a 40% mean loss of climatically suitable area for six southern African bird species by 2050. Coetzee *et al*. (2009) used similar models to examine potential range shifts in 50 species of southern African birds and found that 62% would lose climatically suitable area by 2100, 32% would lose more than half their current area, and 38% would have increasing climatically suitable areas. Barbraud *et al*. (2010) used stochastic population models combining long-term datasets and climate

projections to predict the local extinction of a population of black-browed albatross (*Thalassarche melanophris*) within the next 50 years in the Southern Ocean. These impacts can broadly be categorized as indirect biotically-mediated effects, mainly regulated by changes in resource availability, changing trophic interactions, and competition (Oswald and Arnold 2012).

While indirect effects of climate change have been relatively well studied, there have been few studies of the direct impacts on birds (Oswald *et al*. 2011). Rising environmental temperatures will challenge the thermoregulatory and physiological abilities of endothermic animals at their upper thermal limits (Oswald and Arnold 2012). These direct physiological constraints on endotherms are felt more rapidly than lagged indirect effects. One of the advantages of endothermy is the ability to thermoregulate to maintain internal body temperature at optimal levels in spite of varying environmental conditions. This increases the efficiency of metabolic processes and has allowed endotherms to expand into cold climates (Hayes 2010). However, the ability to maintain thermal homeostasis comes at an energetic cost and inhibits activity at the two extremes of thermal stress (McNab 2002). While endotherms can tolerate decreases in body temperature of up to several degrees without loss of function, they operate near their maximum upper thermal limit and even a small increase in internal temperature can lead to hyperthermia (Speakman and Król 2010, Oswald and Arnold 2012). Hyperthermia can lead to tissue death due to denaturation of cell proteins, and ultimately to the death of the animal (Ritchie *et al*. 1994).

Many seabirds will be particularly challenged by increasing temperatures because they face conflicting thermoregulatory constraints throughout their lives (Kearney 2011). They must have sufficient thermal insulation to withstand heat loss imposed by the cold environments in which they forage and the rapid loss of heat to water when on foraging dives. When nesting on land, however, seabirds are vulnerable to overheating because they

often build their nests in fully exposed areas in the boundary heat layer of the ground (Kearney 2011). They are further constrained because they must stay on the nest to protect the eggs and small chicks from predation and solar radiation. These constraints make them excellent bioindicators of changing thermoregulatory constraints under climate change (Oswald & Arnold 2012).

Seabirds: a trade-off between water and air

Seabirds are subjected to both direct and indirect climate change impacts, but these impacts can be studied separately in seabirds that breed in coastal regions. The nests of these birds are often exposed to the elements, leaving little opportunity to avoid solar radiation. However, they forage at sea, where indirect effects like changes in prey quality and abundance are likely to be felt. Since breeding constrains birds to nesting sites and limits their thermoregulatory options, it seems likely that the ability to dissipate heat has evolved in response to conditions at breeding grounds since birds can roam in search of food or better environmental conditions during the rest of the year.

Diving seabirds have three main energetic costs: homeothermy, flight, and underwater diving (Wilson *et al*. 1992). The more a bird is adapted to reduce one of the costs, the more likely it is to expend energy for the other two, or eliminate it altogether as is the case for flight in some seabirds. When high body temperature needs to be maintained in cold water, heat loss is prevented by a sub-dermal layer of fat and/or air in the feathers. The use of air for insulation is better for flying birds that need to minimize their wing load but it results in high buoyancy, which increases the energetic cost of diving (Wilson *et al*. 1992, Ribak *et al*. 2005). A partly-wettable plumage has evolved in cormorants as a method for reconciling the need for the insulating properties of air with the increased buoyancy it provides (Grémillet *et al*. 2005). The outside part of the feathers can instantly get wet when submerged, reducing the

buoyancy, but the central part remains highly waterproof, providing a thin layer of insulating air. Ribak *et al*. (2005) showed that cormorants can also slow the penetration of water through the feathers by ptilomotion, allowing them a greater flexibility in balancing the energetic trade-offs between thermoregulation and buoyancy.

When ambient temperatures and solar radiation increase, the most direct way to avoid hyperthermia is to move to cooler and/or less insolated areas. However, such movement is not always sufficient for maintaining thermal homeostasis, or it involves costly productivity trade-offs, such as during nesting. In these cases, birds employ a series of behaviours to dissipate excess heat. But these come with costs, which include increased energy expenditure, time-budget trade-offs and increased water loss (Oswald *et al*. 2011). Convection and conduction rates depend on the temperature difference between the surface of the animal and the environment. Increasing the surface area exposed to air, by drooping or propping wings (Bartholomew 1966) is used to increase convective heat loss. Birds may also increase blood flow to the legs and feet though vasodilation, increasing convective heat loss in these extremities (Dawson 1982). Conductive heat loss also occurs mainly through the legs or feet, and is a major source of heat loss in some seabirds (Oswald and Arnold 2012). Since the thermal conductivity of water is 25 times greater than that of air, conductive heat loss can be greatly increased by wetting the body (Wilson *et al*. 1992).

When more passive methods are insufficient to maintain thermal homeostasis, birds can increase heat loss through evaporation. In addition to cutaneous evaporation, the ability to increase ventilation through panting and gular fluttering leads to evaporative water loss being the most effective way of dissipating heat at temperatures above the thermal neutral zone (Dawson 1982, Wolf and Walsberg 1996). Gular fluttering is a rapid movement of the hyoid, which increases air flow over the moist oesophagus, pharynx and the mouth, enhancing evaporative cooling (Lasiewski and Snyder 1969). It has a low energetic cost, but

is costly in terms of water loss; juvenile Cape gannets (*Morus capensis*) were estimated to lose up to 50% of their ingested water after 4 hours of constant gular fluttering, and 100% after 7.5 hours (Hochscheid *et al*. 2002). Because of the increased osmotic stress, evaporative heat loss is used when other behavioural and psychological mechanisms for heat dissipation are typically insufficient (Dawson 1982). The presence of gular fluttering is therefore a good indicator that a bird is becoming heat-stressed and measuring the proportion of time a bird spends gular fluttering may be an effective way of quantifying that stress.

In addition to body positioning and gular fluttering, cormorants also spread their wings to potentially increase thermoregulation ability (Hennemann 1988), although this behaviour is thought to facilitate other functions, such as wing drying (Riijke 1968), digestion (Grémillet 1995), social display and nest shading (Hennemann 1988). If these thermoregulatory mechanisms are not adequate for dissipating excess heat, breeding birds may be forced to either: 1) abandon their nests; or 2) leave their nests for longer periods, increasing mortality by overheating or predation.

Study aims

This study compares the thermoregulatory behaviours of four sympatric cormorant species breeding in southern Africa, crowned cormorant (*Microcarbo coronatus*), Cape cormorant (*Phalacrocorax capensis*), bank cormorant (*Phalacrocorax neglectus*) and white-breasted cormorant (*Phalacrocorax [carbo] lucidus*). A size gradient exists between the four cormorant species, which range from ~800 g for the crowned cormorant to 2.5 kg for the white-breasted cormorant. Large birds have small surface to volume ratios, causing their internal body temperature to respond more slowly to external temperature change than smaller birds (Schmidt-Nielsen 1984). Despite this, it is expected that they will begin gular fluttering at lower temperatures because large birds often begin evaporative heat loss behaviours while well within their thermal neutral zone and smaller birds defer such

behaviours until the upper critical temperature threshold is reached (Maclean 1995). If gular fluttering is initiated at lower temperatures in larger birds, it is expected that they will spend more time gular fluttering and will consequently have higher evaporative water loss. In terms of body position, crouching birds benefit from increased cooling due to increased convection between their legs and the air. They should delay the onset of gular fluttering relative to sitting birds. Key questions include: 1) how does the proportion of time spent gular fluttering change in relation to temperature? 2) Does the onset of gular fluttering vary among species? 3) How is gular fluttering influenced by body position (sitting on the nest or crouching)? 4) How much water do cormorants lose through gular fluttering? 5) How will gular fluttering and water loss be affected by climate change?

METHODS

Study species

The crowned cormorant is endemic to south-western Africa, where it breeds along the coast from Swakopmund, Namibia, in the north, to Tsitsikamma National Park, South Africa, in the east (Hockey *et al*. 2005). The species is one of the smallest southern African cormorants, weighing 730-790 g. It is classified as Near Threatened by the IUCN, mainly because of its small population size (Bird Life International 2012a). Nesting mainly in small groups of 4-50 nests, the world population was estimated at 8 000 individuals in 1982 and is thought to be stable (Hockey *et al*. 2005, Crawford *et al*. 2012). It could be at risk from climate change effects, because of increasing temperatures and a predicted increase in frequency of large storm events, which could threaten the small population. It is a coastal species that feeds on klipfish (Clinidae) and pipefish (Syngnathinae) in estuaries and shallow coastal waters (Rand 1960, Wilson and Wilson 1988). The main breeding season is December - January (Crawford *et al*. 1999a).

The Cape cormorant has recently been uplisted to Endangered by the IUCN as breeding colonies in Namibia and South Africa have undergone rapid population declines over the past three generations (BirdLife International 2013a). Numbers have gone from an estimated > 1 million in the mid-1970s to approximately 285 000 by 2011 (Cooper *et al*. 1982, BirdLife International 2013a). The declines are thought to be attributed to changes in distribution and abundance of its two main prey species, South African pilchard (*Sardinops ocellata*) and Cape anchovy (*Engraulis japonicus capensis*). It is near endemic to southern Africa, and breeds from central Angola to Aloga Bay in South Africa (Hockey *et al*. 2005). Cape cormorants weigh between 1.1 and 1.3 kg. They are known to breed throughout the year, but peak breeding season is October – November (Crawford *et al*. 1999a).

The bank cormorant is endemic to southwestern Africa and is listed as Endangered by the IUCN (BirdLife International 2013b). Total breeding pairs fell from 7 600 in 1980 to 2 800 by 2006, a decline of 53% (Kemper *et al*. 2007). Human disturbance, predation by Cape fur seals (*Arctocephalus pusillus pusillus*) and shifts in the distribution and abundance of their main prey species, the west coast rock lobster (*Jasus lalandii*) are thought to be the main causes of the decline (Crawford *et al*. 1999b, Crawford 2008). Bank cormorants may also be sensitive to increasing temperatures and major storms (Sherley *et al*. 2012). Bank cormorants weight between 1.8 to 2.1 kg (Hockey *et al*. 2005). Peak breeding times are June – July (Sherley *et al*. 2012).

The white-breasted cormorant is the largest cormorant in Africa, weighing approximately 2.5 kg (Nelson 2005). It is common in both coastal and freshwater habitats throughout sub-Saharan Africa. It is not threatened (BirdLife International 2012b). Populations in South Africa are thought to be stable at about 1 200 pairs (Crawford *et al*. 2013). White-breasted cormorants breed throughout the year, with different peak times

depending on the colony location. Peak breeding season at Malgas, Jutten, and Robben Island is October – November, but the peak at Stony Point is May – June (Crawford *et al*. 2013).

Study sites

Four cormorant breeding sites near Cape Town, South Africa were visited in 2012 and 2013 to record nesting behaviour of crowned, Cape, and white-breasted cormorants (Table 1 and Figure 1). All bank cormorant data from three breeding sites in 2012 were provided by J. Roberts (Roberts 2013).

Table 1: Study sites for crowned, Cape, white-breasted and bank cormorants in 2012 and 2013.

	Crowned	Cape	Bank	White-breasted
Robben Island (33°48'S, 18°22'E)	-	2012	2012	-
Jutten Island (33°05'S, 17°57'E)	2013	2013	2012	2013
Malgas Island (33°03'S, 17°55'E)	2012	-	-	-
Stony Point (34°22'S, 18°53'E)	-	-	2012	2012

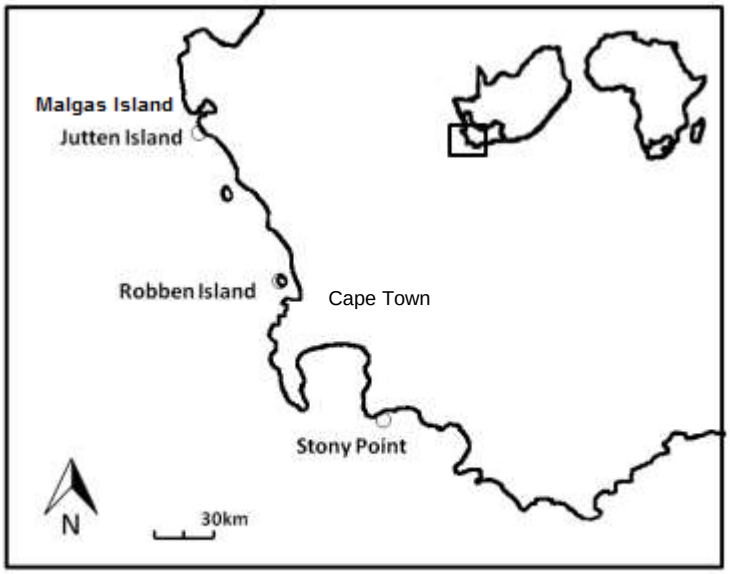

Figure 1: Map of study sites in the Western Cape, South Africa.

At Robben Island, Cape cormorant nests were filmed on the north arm of the jetty at the harbour. The bank cormorant colony was on the south arm. On Jutten Island, the crowned cormorants were nesting in a cluster of small trees approximately 25 m north of the docking area. The bank cormorant colony was situated among large granite boulders along the breakwater, approximately 75 m to the south of the docking area. Cape cormorants were filmed nesting between the crowned and bank colonies. Malgas Island was only visited in December 2012 for filming crowned cormorants. The birds nested on the old jetty and a few nested in the Cape gannet (*Morus capensis*) colony. The Stony Point cormorant colonies are at the western edge of the Betty's Bay Marine Protected Area. Both bank and white-breasted cormorant nests were at the southern end of Stony Point, among the granite boulders near the water edge.

Three Sony Handycam DCR-SX22E cameras set on tripods were used to film selected nests. In 2012, the cameras were connected to a Digital Video Recorder (DVR), and the whole system ran off electricity powered by a generator (Robben) or two car batteries (Jutten, Malgas, Stony Point). In 2013, all video footage was stored on 16 gigabyte SD memory cards and power was provided by the standard battery packs included with the cameras. The memory cards and battery packs lasted approximately 2 hours, after which they were switched for empty memory cards and charged batteries. Filming days varied in length from 4 to 11 hours. . See Appendix 1 for filming dates.

Recording temperature

Both ambient (T_a) and operative (T_e) temperature were recorded at each colony every day with iButtons (model PN:DS1922L-F5#). ColdChain Thermodynamics software was used for programming the iButtons and for downloading data. They were factory calibrated to a resolution of 0.0625^{o}C. The iButtons were programmed to take temperature readings every

10 minutes for the duration of filming. For ambient temperature readings, two iButtons were suspended inside cylindrical Stevenson screens (15 cm high, diameter 13 cm).

To measure operative temperature, simple models were constructed to simulate the temperature which each target species would experience in the absence of metabolic processes or thermoregulatory behaviours. Many such models are constructed by placing taxidermic mounts over a hollow copper cast of the animal (Bakken 1992), however the mounts can be difficult to obtain and tend to be fragile. Walsberg and Weathers (1986) compared operative temperature estimates between mounted specimens and painted metal sphere thermometers for four bird species and found that the average differences were usually less than 2^{o}C over long-term studies (e.g. several hours). Painted metal spheres were used as thermometers in this study because of their durability, ease of construction, and low cost.

Models were assembled from two copper alloy half-spheres, 0.9 mm thick. The size of each sphere was determined by measuring the chest circumference of dead cormorants immediately ventral to the wings (Table 2). The model spheres were manufactured as close to the measured size as possible. A hole was drilled into each lower half-sphere to allow the attachment of wires to hold the two iButtons within each sphere without allowing them to touch the sides or each other (similar to the Stevenson screens). The two half-spheres were then attached using TESA tape and bolted together and painted matte black to imitate the absorbance and reflectance properties of cormorant feathers.

Table 2: Average mass of each species, diameter measured from chest circumference and diameter of cormorant sphere models.

Species	Mass (g)	chest circumference	Model
Crowned	800	8.3	8
Cape	1 200	10.2	10
Bank	2 000	12.1	11.5
White-breasted	2 500	not measured	12.5

One ambient thermometer and one operative thermometer were attached to a concrete block via a metal bar to hold them in place (see Appendix 2). A square of insulating rubber was placed between the thermometers and the metal bars to minimize heat transfer. The thermometers were attached approximately 15 cm above the blocks and a block was placed as close as possible to each colony without disturbing the birds. Since the crowned cormorants on Jutten Island nested in trees, the thermometers were attached to the nearest available tree instead, at approximately the same height as the nests (1 m above ground).

To compare the thermal properties of the operative models, all four species models and one Stevenson screen were deployed in a row from north to south, approximately 50 cm apart. Temperature was recorded by all models over the course of three days in October 2013.

Recording behaviour

Only one nest was recorded at a time for Cape and bank cormorants. Crowned and white-breasted cormorant video included from one to seven nests, mainly due to the shortage of time and cameras at these colonies. In cases where more than one nest was present, all nests were treated as if they were separate videos and assigned the same probability of being selected for analysis. All video footage was broken into 10-minute segments for each nest, to correspond with the 10-minute iButton temperature readings. A random number was assigned to each nest segment using the random number generator in Microsoft Excel. The samples were stratified into 1^{o}C temperature bins and an even number of segments were randomly sampled from each bin to ensure even representation across the range of temperatures. In instances where a segment could not be analysed (e.g. not enough light, camera movement due to wind, etc.), the next sample on the list was taken. In total, 4 044 segments were available for analysis (Table 3). A minimum of 170 segments were analysed for each species. While this accounts for only approximately 15% of the available segments for each species, the time available for watching video was limited.

Table 3: Number of video segments available for analysis and number of video segments analysed.

Species	number of segments	number of segments analysed	percentage analysed (%)
Crowned	1 194	174	15
Cape	804	170	21
Bank	828	173	21
White-breasted	1 218	171	14

The programme JWatcher 1.0 was used to record behaviours from the video footage (Blumenstein *et al*. 2006). This event recorder programme logs the time at which keys are pressed and calculates time budgets and provides summary statistics about the duration of behavioural states and the time intervals between them. A list of all the behaviours of interest was created using the Focal Master tab in JWatcher and a key code was assigned for each (Table 4). Behaviours were defined as being mutually exclusive to each other or capable of co-occurring by using the Focal Analysis Master tab. The video footage was run on Windows Media Player and DVR Player programmes while the Data Capture tab from Jwatcher was running simultaneously. Each key press was recorded by JWatcher, along with the associated behaviour, and the time in the 10-minute segment. The durations of each behaviour for each segment were calculated with the Analysis tab and saved as a results.csv file. The behaviours were then converted to proportions (e.g. the number of seconds for each behaviour/ 600 seconds).

Table 4: Behaviours recorded in Jwatcher and the associated code.

Behaviour	Code
Standing	St
Crouching	Cr
Sitting	Si
Beak open	BO
Beak closed	BC
Head up	HU
Head down	HD
Head tucked	HT
Wings open	WO
Wings closed	WC
Wings propped	WP
Gular fluttering	GF

Data analyis

Temperature data

The two iButton recordings from each thermometer (both ambient and operative) were averaged to obtain one value for each 10-minute video segment. Simple linear regressions were fitted to explain operative temperature as a function of current temperature for each species using the lm function in R (R Core Team 2013).

Behaviour correlations

A correlation matrix of behaviours using Kendall's tau correlation coefficient for proportion of time spent gular fluttering against other behaviours was created in R (R Core Team 2013). Kendall's tau was preferred over Spearman's coefficient because it does not assume a monotonic increase or decrease and easily accommodates ranks of equal values. Behaviours with coefficients > 0.3 were considered to be correlated. Correlated behaviours were not included in the following gular fluttering models.

Gular fluttering models

Gular fluttering was calculated as the proportion of time spent gular fluttering in each 10 minute sampling interval. The distribution of gular fluttering data were highly skewed to both right and left (zeroes and ones). The data were transformed to a binary format, with gular fluttering proportion ≥ 0.5 being given a value of "1" and < 0.5 = "0", such that each observation was classified as gular fluttering or not. To determine which factors influenced the proportion of time spent gular fluttering, a generalized linear mixed model was fit using the lme4 package in R (Bates *et al*. 2013), with gular fluttering proportion as the binary response variable, operative temperature, species and body posture (measured as proportion of time crouching vs. sitting) as fixed effects, and nest as a random effect. Nest was used as a random effect rather than individual bird because the individual on the nest could not be distinguished from its partner. Covariates included in the models were selected *a priori,* based on the aims and predictions of the study. All the selected covariates and the interactions between them were initially fit as fixed effects, and then the dredge function from the MuMIn package in R (Barton 2013) was used to select the best models according to AICc values. Percentage of deviance explained was used to determine the fit of the model, and was given as (deviance of the null model – deviance of the explained model) / deviance of the null model x 100. Both the null model and the fitted models included the random effects.

Gular fluttering threshold temperatures

The moult package in R (Erni *et al*. 2013) was used to determine the threshold operative and ambient temperatures at which each species began gular fluttering and the rate of increase as a function of temperature. The moult package (Erni *et al*. 2013) was designed to estimate the start times and duration of moult in birds. The distribution of gular fluttering was similar to the distribution of feather growth in moulting birds, where there is no feather

growth until a threshold is reached, at which point the feathers grow out until moult is complete. Underhill and Zucchini (1988) developed likelihood models for moult data that are based on four assumptions, modified to suit gular fluttering analyses: 1) the increase in gular fluttering is a linear function of temperature; 2) the temperature range where gular fluttering occurs is the same for each individual; 3) the temperature at which gular fluttering begins (threshold) is normally distributed about a population mean temperature; and 4) the individual observations are independent. Unfortunately, the moult package only allows factors as covariates in the model, and does not allow for random effects. The model included the proportion of time spent gular fluttering as the response variable, with operative temperature as the main explanatory variable, and with species and body posture as fixed effects influencing the threshold (temperature at which gular fluttering begins) and the slope (the rate at which gular fluttering increases with temperature). In this analysis, the proportion of time spent gular fluttering was not a binary variable, it could vary anywhere between "0" for no gular fluttering to "1" for gular fluttering during the whole 10-minute segment. In order to deal with the pseudoreplication from having multiple observations of each nest, nest was added as a fixed effect in the models and the pseudoreplication for both the temperature thresholds and the rates of increase were averaged away (Crawley 2007).

The moult package also allows predictions for the proportion of birds gular fluttering 50% of the time, or 100% of time as a function of temperature (see Erni *et al*. 2013). For the purposes of this paper, the temperature thresholds at which half the birds were gular fluttering all the time was considered to be critical temperatures above which the species was heat stressed.

Modelling evaporative water loss

Water loss due to gular fluttering was estimated using a model modified from Hochscheid *et al*. (2002) which estimates the amount of water lost per hour of gular fluttering by juvenile Cape gannets as a percentage of the total amount of water ingested per day. Water ingestion by juveniles is assumed to be entirely from food. To determine the daily food intake (DFI) for each species, the following equation was used:

DFI = Field metabolic rate (FMR) / energetic value of prey x assimilation rate of prey

The following allometric equation was used to calculate the field metabolic rate (FMR) for each species in kJ/day (Ellis and Gabrielsen 2002):

$$\text{FMR (kJ/d)} = 3.9 \times \text{mass (g)}^{0.871}$$

where 3.9 and 0.871 are constants. Masses used in the equation were 2.5 kg for the white-breasted cormorant, 2.0 kg for bank, 1.2 kg for Cape, and 800 g for crowned. The average energetic value of prey in the calculation of DFI was taken to be 6 kJ/g (Jackson 1990) and the assimilation rate was 77% (Visser 2002). For example, the calculation of DFI for white-breasted cormorant is given by: $3.9 \times 2500\text{g}^{0.871} / (6 \text{ kJ/g} \times 0.7725) = 767$ g of food/day. The water ingested per day was estimated to be approximately 80% of the weight of the prey, so 767 g x 0.8 = 614 ml.

Values for evaporative water loss (EWL) were taken from Lasiewski *et al*. (1966) and are given in mg H_2O/g of body weight/h. Values are 1.82 mg H_2O/g for basal EWL with no gular fluttering, 9.85 mg H_2O/g when gular fluttering 50% of the time, and 12.56 mg H_2O/g when gular fluttering 100% of the time.

Using the estimated daily water intake and the EWL rates calculated by Lasiewski *et al.* (1966), the total percentage of ingested water lost when not gular fluttering, gular

fluttering 50% and 100% of the time were calculated for all four cormorant species. The temperatures thresholds that correspond to gular fluttering 50% and 100% of the time were calculated using the "moult" package above, as described in the "gular fluttering thresholds" section. This allows for estimating the rate of water loss per hour and the temperatures at which each species arrives at these thresholds.

Modelling impacts of climate change on gular fluttering and water loss

Climate change models predict an average global temperature increase of 0.5^{o}C by 2035, 1.3^{o}C by 2065, and 2.2^{o}C by 2100 (IPCC 2013). To determine how such increases would affect water loss in nesting cormorants, gular fluttering proportion was first modelled for each species as a function of the current average temperature, calculated as the average daily maximum temperature during the 2-month breeding peak from 2001-2012 on Robben Island, provided by the South African Weather Service. Then gular fluttering proportions were modelled applying the projected increases of 0.5, 1.3 and 2.2^{o}C to current temperatures. The changes in the proportion of time spent gular fluttering with increasing temperature was then converted to the corresponding amount of ingested water lost per hour.

RESULTS

In total, 515 video segments were analysed for crowned, Cape and white-breasted cormorant behaviours (Table 5). Gular fluttering data were available for 173 bank cormorant video segments.

Table 5: Number of video segments and nests analysed for the study species.

Species	Number of video segments analysed	Number of nests observed
Crowned	174	31
Cape	170	23
Bank	173	21
White-breasted	171	19

Ambient temperatures ranged from 13.2 to 29.6°C, and operative temperature from 13.2 to 38.2°C. See Appendices 2 and 3 for histograms of the number of video segments analysed for each species for each ambient and operative temperature bin.

The operative temperature models heated up and cooled at similar rates (Figure 2). However, the models of the smaller species (crowned and Cape) responded more quickly to ambient temperature changes than the larger ones (bank and white-breasted) (Figure 3). The smaller models responded almost instantly to changes in ambient temperature, but there was a lag of approximately 10 minutes between the small models and the large ones.

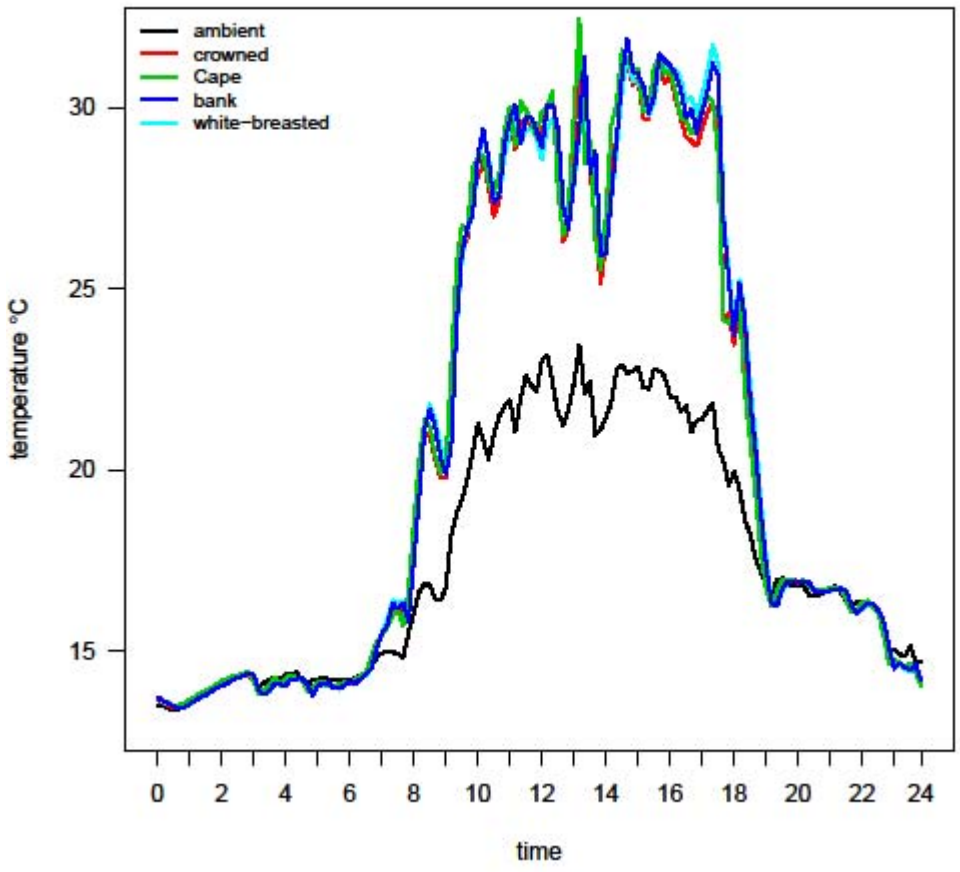

Figure 2: Comparison of operative models and ambient temperature model on Jutten Island on 25 October 2013.

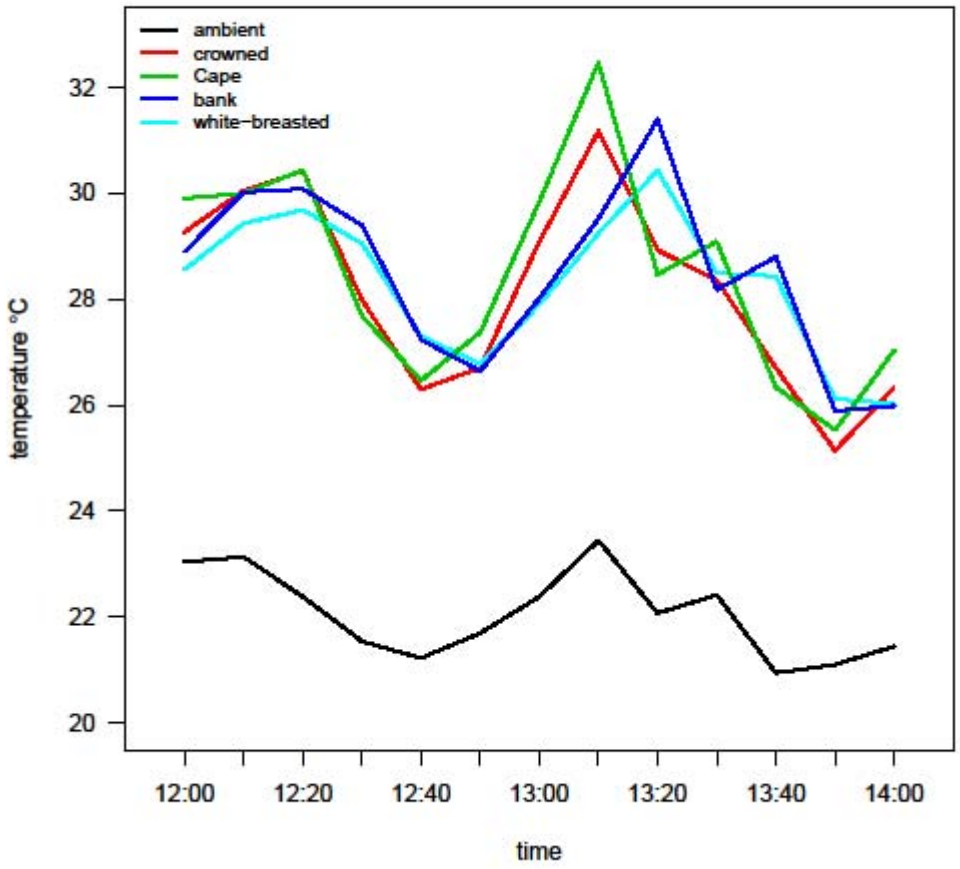

Figure 3: Comparison of operative models and ambient temperature model on Jutten Island from 12:00 to 14:00 on 25 October 2013.

Linear regressions of operative temperature against ambient temperature showed a strong relationship for all species with r^2 coefficients between 0.81 for white-breasted and 0.92 for Cape cormorant (Figure 4). The difference between operative and ambient temperatures increased with temperatures.

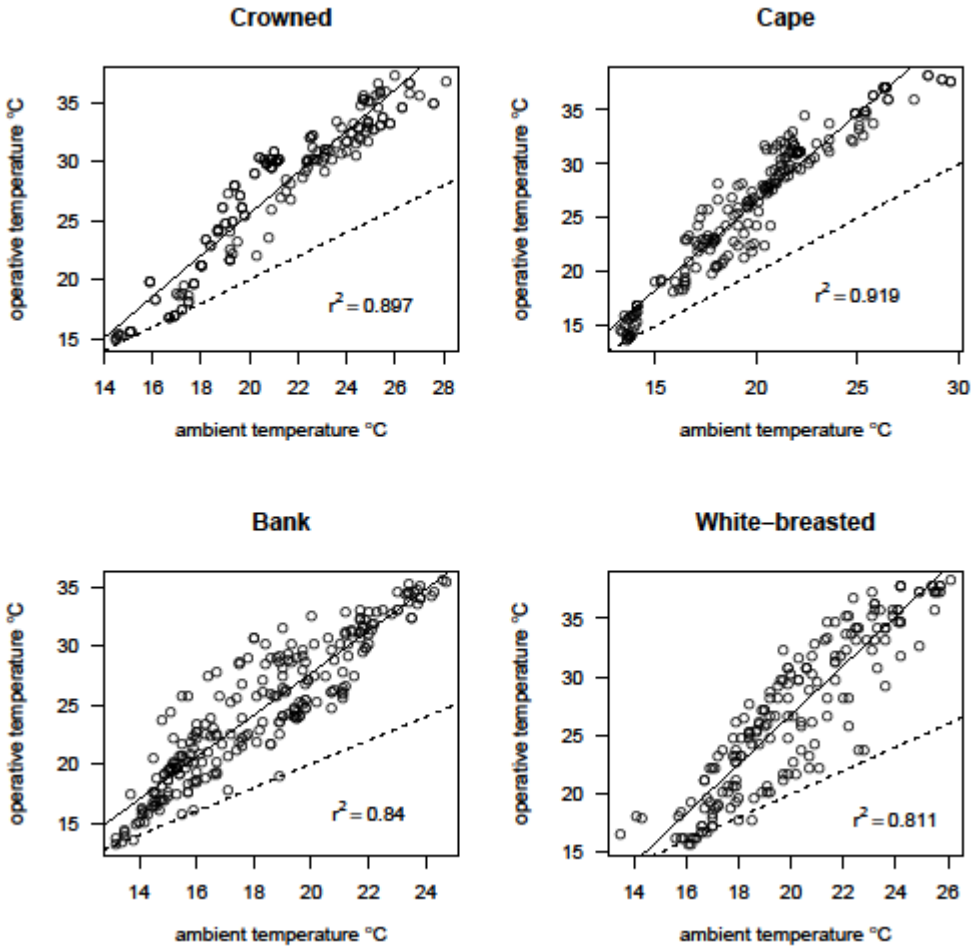

Figure 4: The relationship between and ambient temperature for four cormorant species for all 10 minute samples per species.

There were strong correlations between gular fluttering, and head and beak position for all species (Table 6). Gular fluttering was positively correlated with head up and beak open and negatively correlated with head down and beak closed. Gular fluttering by white-breasted cormorants also was correlated with body posture (Cr and Si), suggesting that they may gular flutter more when sitting than crouching. Wings open behaviour happened so infrequently that it was not included in the correlation matrices.

Table 6: Correlation matrices giving Kendall's tau correlation coefficients for proportion of time gular fluttering against other behaviours of nesting crowned, Cape, bank, and white-breasted cormorants. Bold type indicates coefficents > 0.3. Abbreviations are Si=sit, Cr=crouch, BO=beak open, BC=beak closed, HU=head up, HD=head down, HT=head tucked, WC=wings closed, WP=wings propped, GF=gular fluttering.

	Crowned	Cape	Bank	White-breasted
Cr	0.07	-0.18	0.03	**-0.32**
Si	-0.07	0.18	-0.03	**0.32**
BO	**0.92**	**0.96**	**0.99**	**0.87**
BC	**-0.70**	**-0.73**	**-1**	**-0.68**
HU	**0.8**	**0.62**	**0.59**	**0.84**
HD	**-0.52**	**-0.39**	**-0.47**	**-0.53**
HT	**-0.35**	-0.21	**-0.32**	**-0.43**
WC	0.13	0.07	-0.12	0.2
WP	-0.13	-0.07	0.12	-0.19

Gular fluttering models

Binary models of gular fluttering proportions showed that the model with the lowest AICc value included operative temperature, crouching proportion (CrProp), and species as main effects, and the interaction between operative temperature and species as the final fixed effect (Table 7). The second model had nearly identical AICc, but the first model is preferred because it is more parsimonious. The best model explained only 33.5% of the deviance. In all models, both the crouching proportion and species were selected as important variables in explaining the proportion of time spent gular fluttering.

Table 7: Generalized linear mixed-effects model comparaisons using Aikake's Information Criterion corrected for small sample sizes (AICc) relating gular fluttering proportion (GF) to operative temperature (T_o), body posture (CrProp) and species. For each model, values are given for degrees of freedom (df), AICc, ΔAIC, AIC weight (wAIC) and percentage of deviance explained (%DE).

candidate model	df	AICc	ΔAIC	wAIC	% DE
GF~ T_o+CrProp+species+T_o*species	10	488.2	0.000	0.565	33.3
GF~ T_o+CrProp+species+T_o*species+ T_o*CrProp	11	489.6	1.360	0.286	33.4
GF~ T_o+CrProp+species+T_o*species+ CrProp*species	13	493.3	5.120	0.044	33.5
GF~ T_o+CrProp+species	7	494.2	6.00	0.028	31.6
GF~ T_o+CrProp+species+T_o*CrProp	8	494.9	6.74	0.019	31.8
GF~null	2	705.6	217.35	0.000	-

Gular fluttering threshold temperatures

Models were created to predict the threshold operative and ambient temperature at which at each species begins gular fluttering. For both operative and ambient temperature, white-breasted cormorant begins gular fluttering at the lowest temperature, followed by bank, Cape, and finally crowned cormorant (Figure 5). However, not all thresholds were statistically significant between species (Table 8). The thresholds for the crowned cormorant and bank cormorant, and for the crowned cormorant and white-breasted cormorant did not have overlapping 95% confidence intervals. Although differences between the other species may not be statistically significant, they are biologically relevant and follow the expected pattern with respect to body size. The lack of statistical significance may be a result of the relatively small sample sizes. The rates of increase in gular fluttering were similar for all species except for Cape cormorant, which seems to increase more slowly and has the highest threshold temperature for gular fluttering 100% of the time. The rate for Cape cormorant is even lower when crouching is considered separately (Figure 6).

Since crouching proportion (CrProp) was included in the best model explaining gular fluttering, the thresholds were further broken down by body posture. Thresholds were lower for sitting than for crouching in all cases for both operative and ambient temperature (Figure 6).

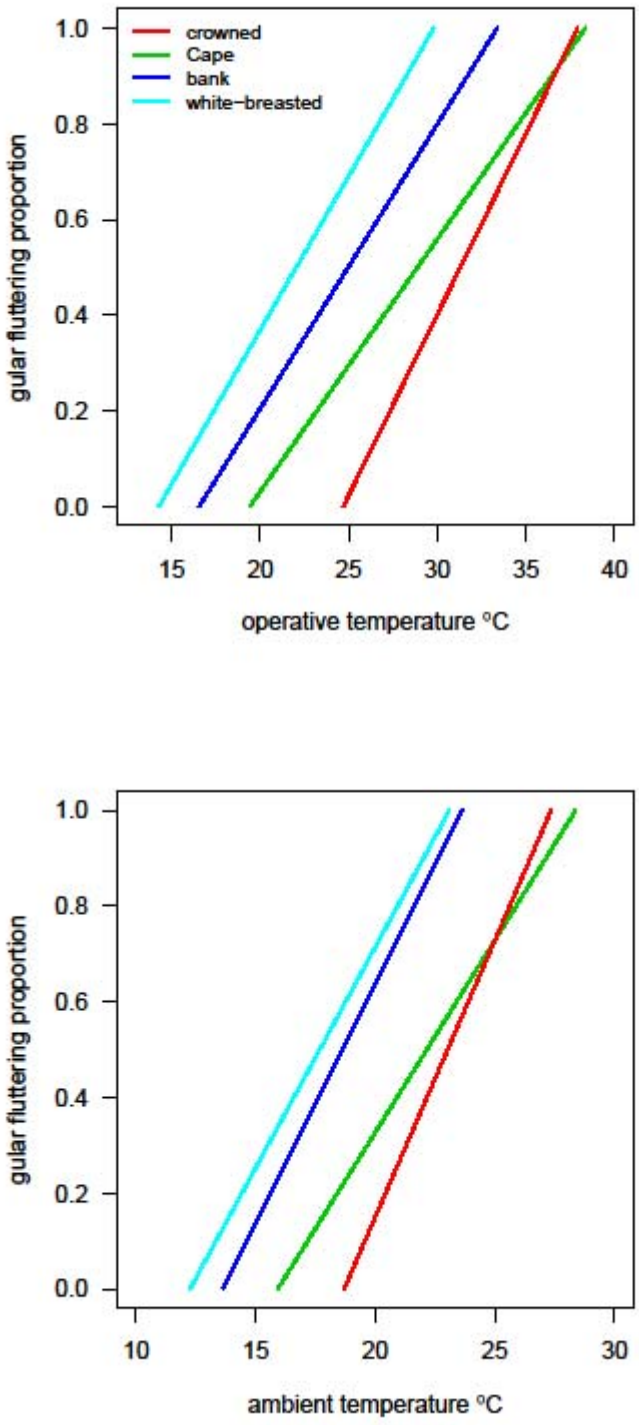

Figure 5: Gular fluttering proportion for crowned, Cape, bank and white-breasted cormorants as a function of operative temperature (top), and ambient temperature (bottom).

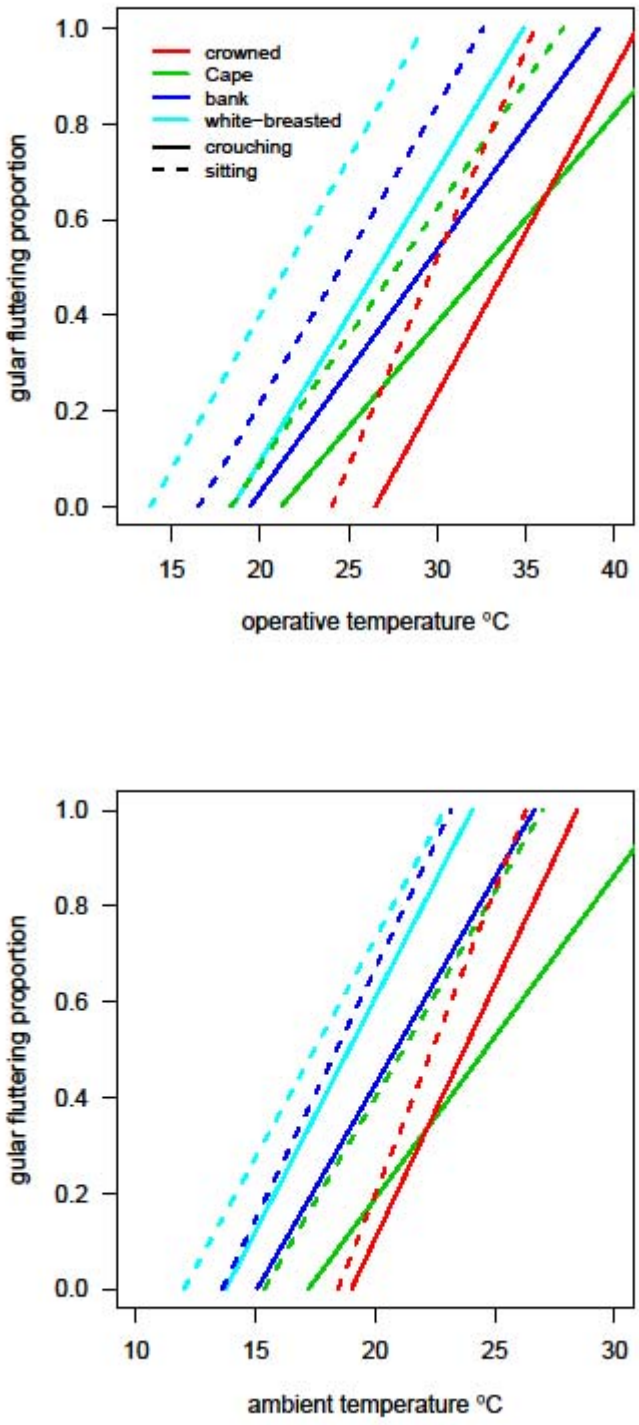

Figure 6: Gular fluttering proportion for crouching and sitting crowned, Cape, bank and white-breasted cormorants as a function of operative temperature (top) and ambient temperature (bottom).

Table 8: Operative and ambient temperature thresholds (± 95% confidence intervals) for the start of gular fluttering for crowned, Cape, bank and white-breasted cormorants.

Species	Operative ^{o}C	Ambient ^{o}C
Crowned	24.69 ± 2.55	18.70 ± 1.88
Cape	19.41 ± 3.47	15.93 ± 2.27
Bank	16.56 ± 3.39	13.64 ± 2.65
White-breasted	14.28 ± 4.57	12.26 ± 3.47

If a cormorant colony is deemed to be stressed when half the birds are gular fluttering all the time, then white-breasted colonies will become stressed first, at an operative temperature of 29.5^{o}C, followed by bank at 33.4^{o}C, crowned at 37.9^{o}C, and finally Cape cormorants at 38.4^{o}C (Figure 6). The corresponding ambient temperatures are 23.1^{o}C for white-breasted, followed by 23.6^{o}C, 27.3^{o}C and 28.4^{o}C for the other species, in the same order. Colonies will reach the threshold at lower temperatures if the birds are sitting compared to crouching (Figure 8).

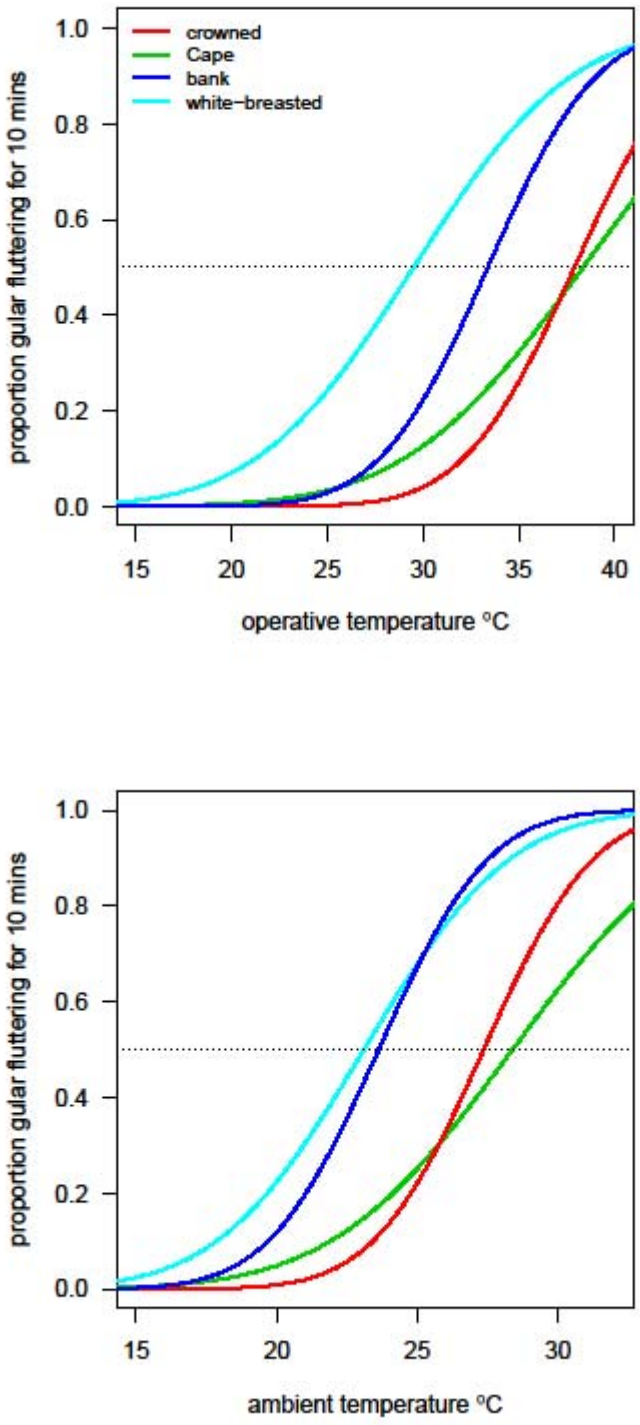

Figure 7: Proportion of birds gular fluttering 100% of the time for bank, Cape, crowned and white-breasted cormorants as a function of operative temperature (top), and ambient temperature (bottom).

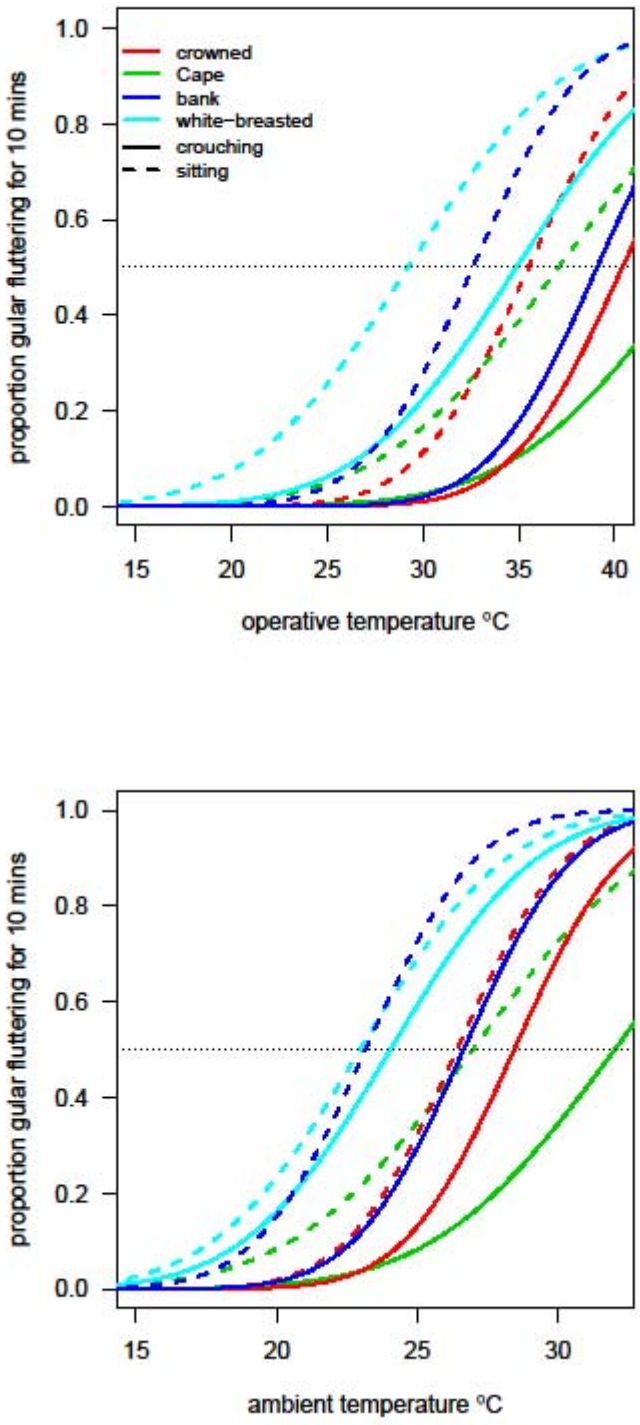

Figure 8: Proportion of birds gular fluttering 100% of the time for crouching and sitting bank, Cape, crowned and white-breasted cormorants as a function of operative temperature (top) and ambient temperature (bottom).

Modelling evaporative water loss

Cormorants lose 25% of their daily ingested water after six to seven hours of intermittent gular fluttering, or approximately five hours if gular fluttering continuously (Figure 9). After seven to eight hours of continuous gular fluttering, they may lose as much as 40% of their daily water intake.

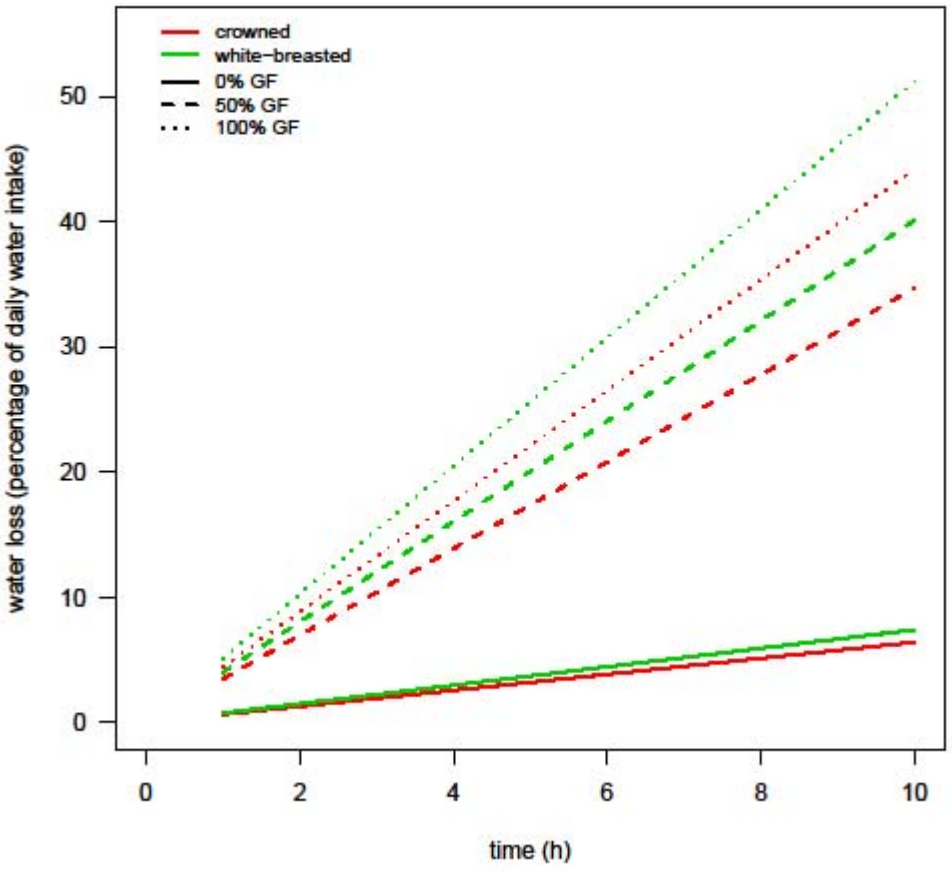

Figure 9: Theoretical water loss as a percentage of daily water ingested and time spent gular fluttering for crowned and white-breasted cormorants. Values for Cape and bank cormorants are not shown but are between crowned and white-breasted cormorant values.

Taking ambient temperature into consideration, white-breasted cormorants will lose approximately 4% of their daily water ingested per hour when the gular fluttering reaches 50% at a temperature of 17.7^{o}C and will reach their maximum when gular fluttering 100% of the time at 23.1^{o}C (Figure 10). Bank cormorant results are similar to white-breasted. Cape

and crowned cormorants begin gular fluttering at higher temperatures and do not reach maximum water loss per hour until approximately 28^{o}C.

Modelling impacts of climate change on gular fluttering and water loss

Both gular fluttering and water loss increased with temperature. Gular fluttering proportion increased by approximately 0.05 for all species with a 0.5^{o}C increase, 0.1 to 0.15 with a 1.3^{o}C increase, and 0.18 to 0.25 with a 2.2 ^{o}C increase (Table 9). The corresponding water loss per hour also increased for all species (Figure 10), with bank cormorant showing the greatest change, increasing by more than 1% per hour of gular fluttering by 2100. This would result in a 9.6% increase in water loss over values in Figure 9 with 8 hours of gular fluttering.

Table 9: Gular fluttering proportion according to current Robben Island daily maximum average temperature during the peak breeding season for crowned, Cape, bank, and white-breasted cormorant, and projected gular fluttering proportion according to temperature increases projected by the IPCC (2013) for 2035, 2065, and 2100.

Species	Current temperature	Projected 2035 temperature	Projected 2065 temperature	Projected 2100 temperature
Crowned	0.69	0.75	0.84	0.95
Cape	0.44	0.48	0.58	0.61
Bank	0.36	0.41	0.49	0.58
White-breasted	0.84	0.89	0.96	1

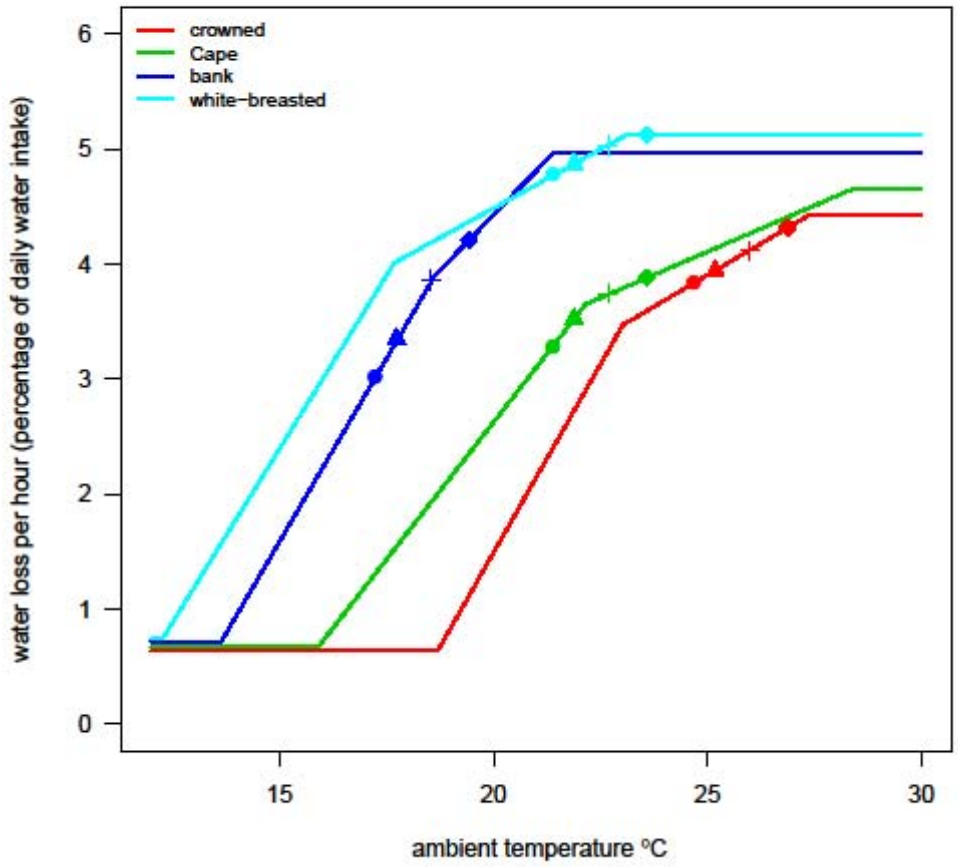

Figure 10: Theoretical water loss per hour as a percentage of daily water ingested in relation to ambient temperature. The first break in each species line represents the gular fluttering starting threshold, the second break represents the ambient temperature at which the species is gular fluttering 50% of the time, and the third break represents the threshold at which the species is gular fluttering 100% of the time. Circles (●) indicate water loss at current Robben Island daily maximum average temperatures during the peak breeding season for each species, triangles (▲) indicate water loss at projected 2035 temperatures (+0.5^{o}C), crosses (+) indicate water loss at 2065 projections (+1.3^{o}C), and lozenges (◊) indicate water loss at 2100 projections (+2.2^{o}C). Temperature projections according to the IPCC (2013).

DISCUSSION

Operative and ambient temperature models

Operative temperatures were always higher at ambient temperatures above 20^{o}C, with the differences between the two being greater at higher temperatures (Figure 4). The

temperatures were closely matched in the cooler early mornings, but the operative temperature models heated up more during the day because of the absorption of solar radiation by the black paint on the spheres. As expected, the smaller models heated up and cooled down more rapidly than the larger ones. For all four species, operative temperature can be predicted from the ambient temperature. The r^2 values were above 0.8 in all cases, and only the white-breasted cormorant was below 0.9.

Although the operative temperature models used in this study may more accurately reflect the temperatures experienced by the birds, they are not perfect. The spheres did not account for the effect of having feathers, and Bakken (1992) suggested that models should be covered by a taxidermic mount to account for the differences in thermal properties that feathers provide. However, given that much of the thermoregulation properties of feathers can be modified by ptilocontrol, or changing the depression or erection of feathers (Bicudo *et al*. 2010), taxidermic mounts alone may not be sufficient to represent much of the thermoregulatory properties of feathers. The models in the study also did not account for heat which may be reflected by the nest or by the presence of nestlings. Older nestlings were often observed gular fluttering from underneath the guarding parent on hot days, likely increasing the temperature being experienced by the parent and the other chicks in the nest. Despite these caveats, the spheres were used in a consistent manner at all colonies during the study. If there were any biases in the data, they were consistent throughout. Bakken and Angilletta (2014) have recognized the difficulty in distinguishing between 2^{o}C temperature increases predicted by climate change and systematic errors of the same magnitude in operative temperature measurements. They recommend that biologists should use detailed physical models calibrated against living animals over potential ranges of postures, orientations and microclimates (Bakken and Angilletta 2014). Future studies on the effects of climate change

predictions on heat stress behaviours in cormorants should consider building more accurate operative temperature models and testing them against actual live specimens.

It may have been appropriate to measure wet-bulb temperature (*Tw*) rather than standard ambient temperature since *Tw* accounts for relative humidity of the air. It is the lowest temperature which may be achieved by evaporative cooling given the relative humidity of the air (Sherwood and Huber 2010). If the ambient air is less than saturated (less than 100% humidity), the *Tw* is lower than the standard temperature. Standard and wet-bulb temperatures are equal at 100% relative humidity. Wet-bulb thermometers can be created by covering a standard thermometer bulb with a wetted cloth and then ventilating it. *Tw* can also be calculated if the barometric pressure and relative humidity are known. For a given temperature, the *Tw* experienced by an animal increases with humidity. Evaporative cooling is less effective as the *Tw* gradient between the bird and the environment is reduced and net conductive and evaporative cooling can occur only if the bird is warmer than the environmental wet-bulb temperature. The standard thermometers used in the study did not account for humidity.

Thermoregulatory behaviours

Correlation matrices were created to avoid collinearity in the behaviour models. Gular fluttering, head position, and beak position were all correlated so only gular fluttering proportion was modelled. The correlations suggest that the beak open position could be used rather than gular fluttering in cases of lower quality video where gular fluttering could not be observed because of lack of resolution or too great a distance to the bird. The birds were rarely observed with an open beak without gular fluttering, which usually commenced within a few seconds. From a conservation standpoint, managers or field staff could rapidly count the proportion of open beaks at cormorant colonies to determine whether birds appear heat stressed rather than having to rely on intensive scanning of individual birds to look for gular

fluttering. The head up position may also be an indicator of gular fluttering, but the birds also adopted this posture when scanning for predators, or to avoid constant begging from hungry chicks.

The Wings Open behaviour was rarely observed. Roberts (2013) also found this behaviour to be rare in nesting bank cormorants. The function of wing-spreading behaviour in cormorants has long been a source of speculation (Cook and Leblanc 2007), but the main functions are thought to be as a drying mechanism for their partially wettable feathers (Sellars 1995) or to warm the birds after ingestion of cold prey (Grémillet 1995). Since this behaviour is well-known in great cormorants (*Phalacrocorax carbo*), of which the white-breasted cormorant is a sub-species, the birds may simply be wing-spreading before arriving at the nest. Another explanation could be that the birds are being subjected to higher-than-normal heat loads while nesting and may actually benefit from having wet feathers as a way of delaying possible heat stress and as a means of cooling chicks. Many birds, including seabirds, have been shown to bathe or wet their feathers when heat-stressed (Maclean 1995, Oswald *et al*. 2008). If cormorants were trading off keeping their feathers wet for the cooling it would provide, it might then be expected that wing-spreading would be more prevalent on cooler days, when the birds are not heat stressed. This has not been shown to be the case however in several cormorant species. Wing-spreading in great cormorants and double-crested cormorants (*Phalacrocorax auritus*) is performed regardless of ambient temperature (Hennemann 1988, Grémillet *et al*. 2003), and is positively correlated with ambient temperature in the flightless cormorant (*Phalacrocorax harrisi*) (Hennemann 1984). Despite this, partially-wettable feathers may allow cormorants another cooling option not available to other birds.

Gular fluttering models

The best gular fluttering model used all the measured variables that were assumed to be important for gular fluttering, the operative temperature, species, body position, and the interaction between operative temperature and species. Body position and species were important variables in all the models that best explained gular fluttering proportion (Table 7) and were used in the subsequent analyses on threshold temperatures. The best model only explained 33% of the deviance, which is relatively low (although many papers have values of less than 5%, see Møller and Jennions 2002). Several reasons could account for this low goodness-of-fit. Two important environmental variables that might influence gular fluttering were not included in the analyses; wind speed and air humidity. High wind speeds would increase convective heat loss, particularly if combined with leg shading and increased blood flow to the legs, reducing reliance on gular fluttering. Evaporative heat loss is higher at low air humidity (Lasiewski *et al*. 1966) making gular fluttering more efficient when there is a greater humidity gradient between the bird and the surrounding air. Relative air humidity is expected to increase with sea surface temperature, a scenario which is predicted by most climate change models (Minschwaner *et al*. 2006). If this occurs, evaporative water loss will be a less efficient means for shedding heat than it is at current relative humidity levels. These models are therefore likely underestimating the amount of time birds will need gular flutter to avoid hyperthermia. Finally, a range of gular fluttering proportions were measured, but were reduced to zeroes and ones in order deal with data distribution problems. This loss of information may have influenced the percentage of deviance explained by the models.

Gular fluttering threshold temperatures

Gular fluttering threshold temperatures essentially followed the predicted patterns. Gular fluttering increased with temperature for all the species. The larger cormorants (white-breasted and bank) initiated gular fluttering at lower temperatures than Cape and crowned

cormorants and reached the maximum at lower temperatures as well. This was expected, since the larger birds typically initiate evaporative water loss before being heat-stressed (Maclean 1995) and cool off slower because of their relatively small surface to volume ratio (Schmidt-Nielsen 1984). Interestingly, the slope of the increase in gular fluttering proportion with temperature was smaller for Cape cormorant compared to the other species, which all had similar values. The threshold at which Cape cormorant began gular fluttering was lower than for crowned cormorant despite the two species being similar in size and mass, while the larger bank and white-breasted cormorants had very similar starting threshold temperatures (within 1^{o}C). This suggests that Cape cormorants may begin gular fluttering earlier than strictly necessary. Maybe this is an early response to the longer foraging trips that Cape cormorants must now make in colonies north of Cape Point (Hamann *et al*. 2012), likely as a result of changes in prey distribution and availability (Coetzee *et al*. 2008). Hamann *et al*. (2012) showed that Cape cormorant colonies north-west of Cape Point had significantly longer foraging trips than those to the east, which means longer periods sitting on the nest without being able to cool. Initiating gular fluttering slightly earlier may confer a thermoregulatory advantage in long run, particularly on sunny days when the temperature is likely to be higher. This could be tested by repeating this experiment on colonies in to the north-west of Cape Point and on colonies to the east.

When body position was included in the model, the gular fluttering proportion was higher for sitting than crouching for all species. Crouching birds likely benefitted from increased convective heat loss and therefore only gular fluttered at higher temperatures. Not only did crouching birds benefit from convection heat loss from the legs, but also from having their wings propped, a behaviour which was positively correlated with crouching. Propping the wings exposed the large blood vessels connecting the wings to the body to increase airflow, likely helping to cool the birds through convective heat loss (Maclean

1995). The fact that gular fluttering proportion was higher for sitting birds suggests that cormorants are most at risk of heat stress while incubating, when they must sit on the nest and may not have the option of crouching. Gular fluttering may be the only behavioural option for cooling down at this point. Once the nestlings are sufficiently large and can thermoregulate, crouching over the nest and shading the hatchlings with the wings allows the cormorants to reduce heat stress while still providing adequate shade for the nestlings on hot days.

Modelling evaporative water loss

Hochscheid *et al*. (2002) showed how juvenile Cape gannets were estimated to lose approximately 50% of their ingested water after only 4 hours of gular fluttering. This study suggests that water loss estimates for adult cormorants are lower than for juvenile Cape gannets. The differences can partly be explained by the differing ways of calculating the amount of ingested water. Hochscheid *et al*. (2002) estimated that the gannets consumed 500 g of fish per day, whereas an allometric equation for field metabolic rate was used here to calculate daily food intake. Nevertheless, evaporative water loss from gular fluttering in cormorants is still high. Cormorants lose approximately 40% of their daily ingested water after 8 hours of gular fluttering. This represents about 10% of their total body weight. This amount does not include the water lost in the faeces. Most birds can lose between 30 to 40% of their body weight in water before dying (Maclean 1995). Whereas it is not likely that cormorants would become dehydrated and die after one day, several consecutive days of water deficit could eventually lead to death of the chicks and could force adults to abandon nests. Considering that large cormorants begin gular fluttering at relatively low ambient temperatures, their water loss can be high even on mildly warm days (~ 20^{o}C ambient temperature). Fortunately, cormorants do not usually make long foraging trips like the Cape gannet. Cape gannet foraging trips can last from 8 to 22 hours (Grémillet *et al*. 2004) while foraging trips for cormorants are much shorter, with Cape cormorants having the longest

among the four species at 1.25 to 4.5 hours (Hamann *et al*. 2012). They are therefore unlikely to have nest attending bouts of eight hours or more.

Heat stressed great skuas (*Stercorarius skua*) in the Northern Hemisphere have been observed leaving nests to bathe and to drink fresh water, presumably to cool themselves and to avoid dehydration due to increased evaporative water loss (Oswald *et al*. 2008). If cormorants were to adopt this behaviour, it would likely have serious reproductive consequences in the colonies visited in this study. Kelp gulls (*Larus dominicanus*) and sacred ibis (*Threskiornis aethiopicus*) are major predators of cormorant eggs in those colonies. Gulls ate Cape cormorant eggs on Jutten Island within seconds of them being exposed, sometimes while both parents were present attempting to switch incubation duties (pers. obs.). In some extreme cases, adult seabirds have even been shown to die of dehydration during incubation at abnormally high environmental temperatures (Gaston *et al*. 2002). While adult cormorants may drink water on the way to and from the nest to prevent dehydration, juveniles depend entirely on water ingested through food and are thus more susceptible to dehydration.

The increasing temperatures that are projected in climate change models will have serious consequences for nesting cormorants. Gular fluttering could increase by as much as 25% by 2100, further stressing the birds during the breeding season. Hourly water loss rates could increase as well, by as much as 1.5% of daily ingested water per hour of gular fluttering. These predictions are likely to be very conservative since the temperatures used for modelling are projected global averages over land and water, and increases over land are expected to be greater (IPCC 2013). Furthermore, the frequency and duration of extreme high temperature events have been increasing over the past 50 years (New *et al*. 2006, Kruger and Sekele 2013). This will likely have more serious consequences if they occur during the breeding season than will relatively small overall global temperature increases.

Future studies

This study did not look at the effects of the standing posture on gular fluttering in cormorants. The birds only tended to stand when the chicks were older and the adults could no longer crouch over them. Unfortunately, most of the video footage was recorded early in the breeding season for each species, and while there were some video samples with the standing behaviour, there were too few for analysis. Spreading the recording days out through the breeding season would allow for more samples of standing birds. Standing birds may initiate gular fluttering at lower temperatures than crouching ones since they probably benefit even more from convective heat loss, particularly on windy days.

This study also did not consider the orientation of the birds relative to the position of the sun (Roberts 2013). Incubating common nighthawks (*Chordeiles minor*) have been shown to orientate their bodies away from the sun during hot days as a means of shading the throat and possibly reducing evaporative water loss (Weller 1958). Double-crested cormorants and great cormorants orientate their backs towards the sun after feeding and adopting the wing-spreading posture (Sellars 1995, White *et al*. 2008), although this behaviour is thought to be more related to drying the feathers. On windy days, double-crested cormorants preferred orientating themselves facing the wind, regardless of the position of the sun (Sellars 1995) suggesting that convective cooling may outweigh evaporative cooling on days of partial cloud cover. Bartholomew and Dawson (1979) showed that incubating Heerman's gulls (*Larus heermanni*) orientated into the wind when under conditions of low solar radiation, but did not show an orientation pattern on days of high solar radiation (Bartholomew and Dawson 1979). The authors suggested that the difficulty of moving the eggs and readjusting them to the brood patch more than offset the advantage of the diminution in heat gain resulting from shifting away from the sun.

Finally, future studies should consider using wet-bulb temperature measurements rather than standard temperature because wet-bulb temperature accounts for the lower rates of evaporative cooling when relative humidity is higher. Since the effectiveness is evaporative cooling (i.e. gular fluttering) is less at higher humidity levels, the gular fluttering rates and corresponding water loss measured in this thesis are surely underestimated.

Conclusions

This study has shown that gular fluttering increases with temperature in crowned, Cape, bank and white-breasted cormorants, as was expected. The size of the birds has an effect on the temperature thresholds at which each species begins gular fluttering behaviour, with the largest gular fluttering first. The body position of nesting birds also influences gular fluttering, with crouching birds likely benefitting from increased convective cooling compared to incubating birds, leading to relatively lower gular fluttering. And finally, gular fluttering leads to important water loss in cormorants, with the increased water loss beginning at lower temperatures for the larger species.

These findings indicate that more extensive heat waves from climate change may have serious direct impacts on nesting cormorant colonies in southwest Africa. Climatic warming may raise temperatures beyond those tolerable to cormorants, particularly during the breeding season, when the less costly thermoregulatory options are not always available. This study has shown that birds might be most vulnerable during the incubation stage since gular fluttering is one of the only options available to incubating birds for dissipating heat. It is also the breeding stage where birds are more likely to abandon nesting, since the amount of energy investment at that point is low relative to later in the breeding cycle. Some species may be able to shift their breeding dates to compensate for increasing temperatures, but if they time their breeding activities to coincide with peaks in their main prey species, as is the case with Cape cormorants (Crawford and Dyer 1995), shifting breeding dates may result in

poorer diets or increased competition from other species. Cape cormorants have been known to defer breeding until Anchovy become more readily available, in which case dietary issues may not be a concern, but if breeding is delayed until the summer months (January to March), the birds will have a much higher risk of enduring heat stress. Bank cormorants already breed during the coldest months (June – July) and do not have the option of breeding at cooler times of the year. Bank cormorant may therefore be the most at risk from climate change and heat stress among the four species studied, simply because of a lack of available options during the breeding season to deal with increasing temperatures.

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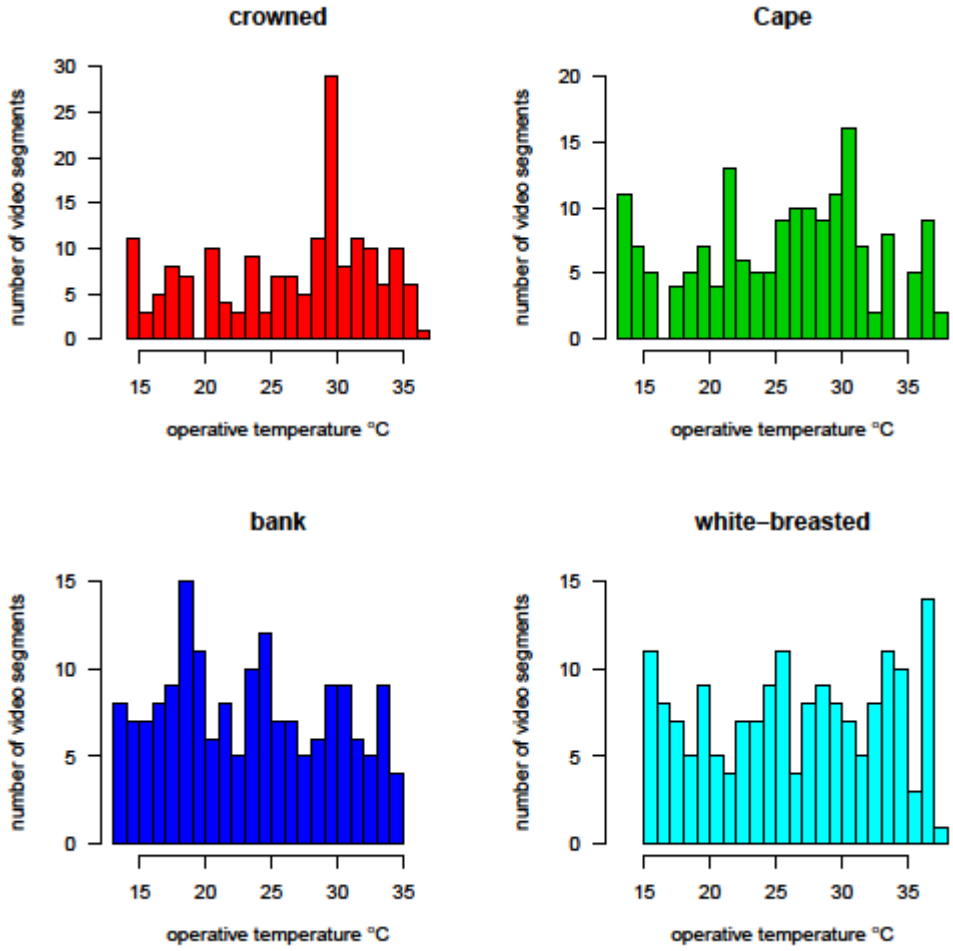
APPENDICES

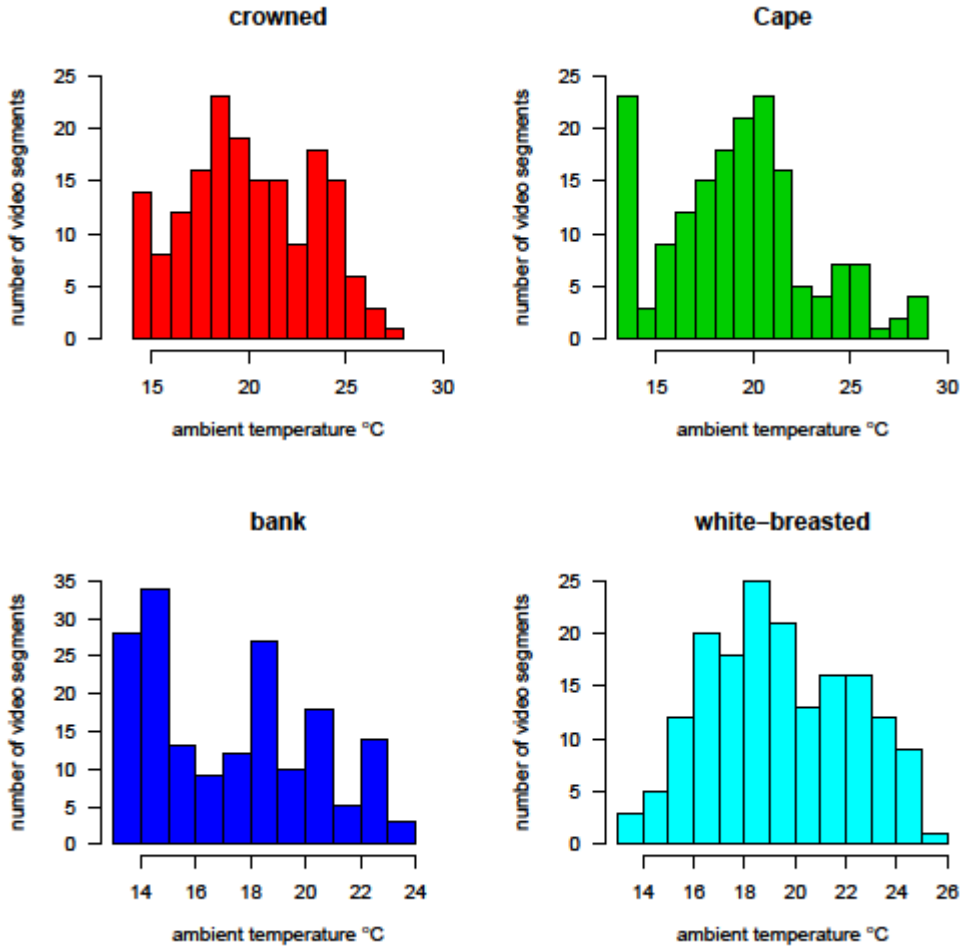
Appendix 1: Filming days for crowned, Cape, bank, and white-breasted cormorants at Malgas Island, Jutten Island, Robben Island, and Stony Point in 2012 and 2013.

Species	Location	Dates
Crowned	Malgas	9-14 December 2012
Crowned	Jutten	23-26 October 2013
Cape	Robben	1, 2, 4, 6, 7, 10-14 October 2012
Cape	Robben	1-4 November 2012
Bank	Robben	17, 18,19 April 2012
Bank	Robben	30 May 2012
Bank	Jutten	11, 12, 13 June 2012
Bank	Jutten	3, 4, 5, 24, 25 July 2012
Bank	Stony Point	10, 11, 16-18, 30, 31 May
Bank	Stony Point	11, 30 July
Bank	Stony Point	2, 3 August
White-breasted	Stony Point	30, 31 May 2012
White-breasted	Stony Point	1, 19, 28 June 2012
White-breasted	Stony Point	11, 30 July 2012
White-breasted	Stony Point	2, 7 August 2012
White-breasted	Jutten	24, 25 April 2013
White-breasted	Jutten	5, 6, 20-22 May 2013
White-breasted	Jutten	6 June 2013

Appendix 2: Ambient thermometer on left, operative thermometer on the right (photo Jenni Roberts).



Appendix 3: Number of samples (video segments) as a function of operative temperature for crowned, Cape, bank and white-breasted cormorants.



Appendix 4: Number of samples (video segments) as a function of ambient temperature for crowned, Cape, bank and white-breasted cormorants.