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Storms and heat limit the nest success of Bank Cormorants: implications of future climate change for a surface-nesting seabird in southern Africa

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Abstract The Bank Cormorant *Phalacrocorax neglectus* is endemic to the Benguela Upwelling System of southern Africa. Most breeding colonies occur on offshore rocks, islands or man-made structures close to the high-water mark. Despite adaptations for breeding close to the water, nests can be lost to storms. Using data from two colonies where food is not considered limiting, we present a comparative study on nest survival in Bank Cormorants. Using a combination of the Mayfield method and parametric survival analysis, nest success was compared in nests on man-made structures at Robben Island, South Africa, where birds breed during the austral winter, with nests on man-made and natural structures at Mercury Island, Namibia, where Bank Cormorants breed during the austral summer. Overall, the probability of a nest surviving the breeding attempt was lower at Robben Island than at Mercury Island in all three seasons. Nest failures at Robben Island were related to wave heights and air temperature, with trends to suggest reduced

chick survival in years where major storm events occurred during peak breeding. A heat wave appeared to cause major chick mortality at Mercury Island in 2005. Nest survival was relatively invariable between years at the main site monitored on Mercury Island, where nests were partially sheltered from the sun, but breeding productivity was poor in comparison to other cormorant species. Winter breeding in South Africa may increase the risk from storms but reduce the risk of heat exposure. An understanding of the impact of stochastic events on Bank Cormorants may be important in safe-guarding the continued survival of the species, particularly in light of the risks posed by future climate change.

Keywords Reproductive success · Nesting habitat · Climate change · Seabird conservation · Bank Cormorant · *Phalacrocorax neglectus*

Zusammenfassung

Stürme und Hitze limitieren den Bruterfolg der Küstenscharbe *Phalacrocorax neglectus*: Auswirkungen des Klimawandels auf einen nahe des Meeresspiegels brütenden Seevogel im südlichen Afrika

Die Küstenscharbe *Phalacrocorax neglectus* ist endemisch für das Auftriebsgebiet des Benguela-Stroms im südlichen Afrika. Die meisten Brutkolonien befinden sich auf Felsen, Inseln und künstlichen Strukturen kurz über der Hochwasserlinie. Trotz Anpassungen an das Brüten nahe der Wasserlinie werden Nester oft durch Stürme zerstört. In dieser Studie vergleichen wir den Bruterfolg der Küstenscharbe in zwei unterschiedlichen Kolonien, in denen keine Nahrungsknappheit vorliegt. Mit Hilfe der Mayfield-Methode und parametrischer Tests zur Berechnung der

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Überlebensrate wurden der Bruterfolg von Tieren auf Robben Island, Südafrika, und Mercury Island, Namibia verglichen. Auf Robben Island brüten die Tiere im dortigen Winter auf künstlichen Strukturen, während die Vögel auf Mercury Island während der Sommermonate sowohl auf natürlichen als auch auf künstlichen Strukturen brüten. In allen drei Untersuchungsjahren lag der Bruterfolg auf Robben Island unter dem von Mercury Island. Nestverluste auf Robben Island wiesen einen Zusammenhang mit Wellenhöhe und Lufttemperaturen auf und höhere Kükenverlusten wurden in Jahren beobachtet, in denen große Sturmereignisse mit der Hauptbrutperiode zusammenfielen. Eine Hitzewelle in 2005 verursachte ein großes Kükensterben auf Mercury Island. Der Bruterfolg schwankte nur gering auf Mercury Island in der Hauptbrutkolonie, wo Nester teilweise geschützt und im Schatten lagen. Im Vergleich zu anderen Kormoranarten war der Bruterfolg aber eher gering. Das Brüten im Winter bei Tieren in Südafrika verringert die Gefahr der Verluste durch Hitzewellen, erhöht aber die Gefahr von Nestverlusten durch Stürme. Ein besseres Verständnis der Einflüsse von stochastischen Wetterereignissen auf den Bruterfolg dieser bedrohten Art ist besonders wichtig in Hinblick auf den Klimawandel und damit einhergehenden Veränderungen im Wetter.

Introduction

The Bank Cormorant *Phalacrocorax neglectus* is an endemic marine cormorant within the Benguela Upwelling System of southern Africa (Crawford and Cooper 2005). The species is considered ‘Endangered’ (BirdLife International 2010) following a decrease in the overall population from c. 9,000 breeding pairs between 1975 and 1981 (Cooper 1981; Crawford et al. 1999) to a maximum of 3,600 pairs by 2007 (Crawford et al. 2008a). In both South Africa and Namibia, large reductions in the number of Bank Cormorants breeding have coincided with changes in the biology of their main prey species (Kemper et al. 2007; Crawford et al. 2008a). However, baseline data on several key population parameters are sparse for Bank Cormorants (e.g. adult survival, breeding success; see Crawford and Cooper 2005) and the exact relationships between prey quality or availability and population trends are not well understood in all cases (Crawford et al. 2008a; Ludynia et al. 2010a).

In South Africa, Bank Cormorants are thought to principally prey on West Coast Rock Lobster *Jasus lalandii* (Cooper 1985; Crawford and Cooper 2005), although fish makes up most of the diet at some colonies (e.g. Dassen Island; Crawford and Cooper 2005). Decreases at most

South African colonies north of Cape Town between 1978 and 2006 coincided with reduced growth rates of Rock Lobster and a shift in its distribution (Cruywagen 1997; Crawford et al. 2008a). In contrast, the population at Robben Island, which is situated in an area declared as a Rock Lobster sanctuary in the 1960s (Pollock 1987), increased from c. 60 pairs in 1978 to c. 130 pairs in 2006 (Crawford et al. 2008a), suggesting that food was not limiting that colony. Similarly, prey availability to Bank Cormorants breeding at Mercury Island, the largest colony in Namibia, was considered to be adequate during the late 2000s (although the prey was of low energy content; Ludynia et al. 2010a, b), and in 2006, the island held around 55% of the global population (Kemper et al. 2007; Crawford et al. 2008a).

Besides being constrained by food availability, the distribution of seabird breeding colonies along the southern African coastline is also influenced by the availability of sites free from disturbance and protected from land-based predators (Berruti 1995; Bartlett et al. 2003). Consequently, Bank Cormorant colonies tend to occur on offshore islands, mainland cliffs (e.g. Bartlett et al. 2003) or high boulders and stacks along rocky shores. They also make use of man-made structures such as guano platforms, piers and harbour walls (Williams 1987; du Toit et al. 2003). Human disturbance, including through harbour development, has caused the desertion of at least four Bank Cormorant breeding colonies and reduced numbers at six others (Crawford et al. 1999). At Robben Island, breeding is restricted to the harbour walls and an old, disused jetty, probably as a result of the level of human activity on and around the island (see, e.g., Crawford and Dyer 2000, pp. 1–4).

Bank Cormorants build relatively large, heavy nests close to the water’s edge using wet seaweed (Cooper 1986). The seaweed becomes “plastered” to the rock surface and the birds also defecate onto the side of the nest, causing the outside to become covered in a hard crust of guano (Cooper 1986). These characteristics have been suggested as prerequisites for breeding close to the sea (Cooper 1986). However, despite these adaptations, whole nests and their contents can be lost to storms (Cooper 1986). Crawford and Cooper (2005) noted that 5% of 292 nests were washed away by sea storms, but gave no further details. Such losses had been observed at Robben Island prior to this study, but had not been quantified (R.B.S., personal observation).

This paper presents a comparative study on nest survival in Bank Cormorants from Mercury Island, Namibia, and Robben Island, South Africa. By using data from two colonies where food was not considered to be limiting the population (see above), we provide baseline information on the breeding productivity of Bank Cormorants. To quantify

the impact of winter storms, we compare nest survival rates at Robben Island, where birds breed during the austral winter (Crawford et al. 1999) on man-made structures close to the water, with survival rates at Mercury Island, where Bank Cormorants breed during the austral summer (Crawford et al. 1999). In addition, by relating breeding failures to sea-state and weather data, we document the influence of environmental variability on the breeding success of Bank Cormorants and discuss how understanding the impact of stochastic events may be important for the continued survival of the species in light of the risks posed by future climate change.

Methods

Study sites and nest monitoring

Nest monitoring periods were 30 November 2004 to 22 May 2005 (hereafter ‘2004/05’), 20 December 2007 to 2 May 2008 (‘2007/08’) and 29 October 2009 to 8 April 2010 (‘2009/10’) at Mercury Island (25°43’S, 14°50’E; Fig. 1).

At Robben Island (33°48’S, 18°22’E; Fig. 1), nest checks were made from 21 March to 9 August 2007, from 26 April to 8 August 2008 and from 11 March to 18 September 2009. Monitoring was aimed to begin prior to the main period of egg laying; however, at both colonies, eggs were present in some nests at the first check. Nests found prior to or during incubation were included in the study and nests were added to the study throughout the monitoring period. Nests were identified at each visit by reference to photographs or sketches made from fixed locations.

Nests were monitored at two of the three breeding locations on Robben Island, a disused old jetty (OJ; Fig. 1) and the long arm of the Murray’s Bay Harbour wall (LA; Fig. 1). At both sites, nests were on man-made structures and were exposed to sun, wind, rain and potential wave action. Nests on the OJ were all at an elevation of c. 4 m. Nests on the LA were between c. 2 and c. 10 m from the water (all elevations are estimates based on high tide). At Mercury Island, nests were monitored on the Main Jetty (MJ; Fig. 1) in all 3 years, as well as at a number of other sites which held smaller colonies in 2004/05 and 2009/10. In 2004/05, nests were studied at two additional man-made

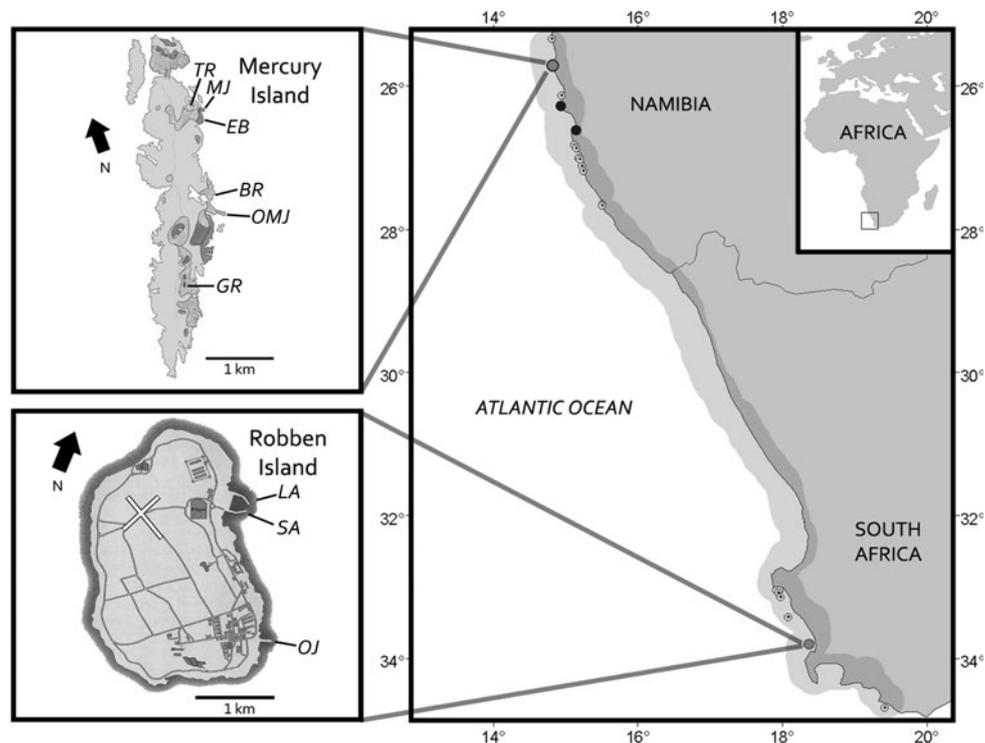


Fig. 1 The locations of Mercury Island and Robben Island along the southern African coastline in relation to the approximate extent of the Bank Cormorant *Phalacrocorax neglectus* breeding distribution (indicated by grey shading). At Mercury Island, nests were monitored at the Main Jetty (MJ), Toilet Rock (TR), the Old Main Jetty (OMJ), the Eastern Buttress (EB), Gannet Rock (GR) and Bird Rock (BR), and swell and winds predominated from the south during the monitoring periods.

At Robben Island, Bank Cormorants bred on a disused old jetty (OJ), and the long (LA) and short-arm (SA) of the Murray’s Bay Harbour; swell and wind predominate from the north and north-west in Table Bay during winter. Circle with dot extant colonies <100 breeding pairs, grey circle the two study colonies, which host c. 1,800 (Mercury) and c. 130 (Robben) pairs, black circle other extant colonies >100 breeding pairs (count data from Kemper et al. 2007)

sites, Toilet Rock (TR) and the Old Main Jetty (OMJ) and at three additional natural sites, the Eastern Buttress (EB), Gannet Rock (GR) and Bird Rock (BR). In 2009/10, the two additional sites were the OMJ and TR. At Mercury Island, nests were either at elevations of c. 5 m (TR, OMJ, EB, BR) and were potentially exposed to wave action or c. 10 m (MJ, GR), where the elevation meant that they were above all but the most severe swells. All sites were exposed to sun, wind and rain except the MJ, where the jetty structure provided shade from the sun for most of the day. At all sites, human disturbance to the study nests was minimal between monitoring visits.

The target for monitoring visits was 7 days, but occasionally nests were checked at intervals of 2–3 weeks. On each visit, the number or presence of eggs or the number and approximate size of any chicks were recorded where possible (see below). Chicks were classified into five stages of development: newly hatched chicks—no down, less than 6 days old (Crawford and Cooper 2005); small downy chicks—still sheltering under the adult, less than half the adult size; medium downy chicks—over half adult size to about 3/4 adult sized; large downy chicks—over 3/4 adult sized, body still covered in down; and woolly necks—full size of the adult, flight feathers on the body, down on the neck and head. A chick was considered to have fledged if it was seen on the nest with all the down lost on the head and neck (termed a fledgling) or if it was seen at the nest as a woolly neck on at least two occasions. If more than one chick was present, the point of fledging for the nest was based on the last chick to reach the above criteria. The chicks in this study were not colour ringed and chicks may leave the nest for short periods after 50 days (Crawford and Cooper 2005). At Mercury Island, once the chicks reached the age of large downy chicks or woolly necks, they occasionally left the nest and formed small groups. In these instances, the group members were assigned to nearby nests according to the age and number of chicks present on the previous visit. Thus, nest success may have been overestimated.

After a breeding attempt failed or succeeded, nest sites were still checked until the end of the monitoring period in case the nest owners initiated another breeding attempt or the chicks had just been absent from the nest at the last check. Double brooding has been recorded in Bank Cormorants (Crawford and Cooper 2005), so eggs laid in a nest following a completed breeding attempt were assumed to be second clutches, while eggs laid into a previously empty nest were classified as first clutches. Consequently, some clutches may have been misclassified.

In 2007 and 2009, an active nest count was conducted monthly at Robben Island. Nests on the LA and OJ were counted during a normal monitoring visit. The nests on the short arm of the harbour (SA; Fig. 1) were counted from

the LA using binoculars. A nest site was defined as active if there were adults or chicks in attendance, or if fresh nesting material was present (Cooper 1981). For most counts, the number of nests that contained eggs or chicks was recorded for the LA and the OJ. Pairs of adults defending a potential nest site were not counted (cf. Crawford et al. 1999).

Weather and sea-state data

Daily values for average wind direction ($^{\circ}$ from north), average wind speed (ms^{-1}), speed of the maximum wind gust (ms^{-1}), direction of the maximum wind gust ($^{\circ}$ from north), maximum and minimum temperature ($^{\circ}\text{C}$), average temperature ($^{\circ}\text{C}$) and rainfall (mm) were obtained for Robben Island from weather station 0020618X (located 2 m above the ground at $33^{\circ}47'\text{S}$, $18^{\circ}22'\text{E}$). During the period of nest monitoring, the maximum and minimum temperatures ranged from 12.0 to 32.5 and 5.0 to 17.9 $^{\circ}\text{C}$, respectively (mean 18.6/11.7, SD 3.3/2.5), daily rainfall ranged from 0.2 to 68.8 mm (mean 5.8, SD 8.6) on days when rain some rain fell, and the speed of the daily maximum wind gust ranged from 3.8 to 26.3 ms^{-1} (mean 10.2, SD 3.8).

Sea-state data were captured in 3-h intervals (from midnight) by WaveNet (<http://wavenet.csir.co.za>) station CP01 (the closest to Robben Island, located at Cape Point, $34^{\circ}20'\text{S}$, $18^{\circ}28'\text{E}$, in 70 m depth of water). The parameters retrieved from the dataset were significant wave height (H_s , mean height of highest 1/3 of all waves in metres); extreme wave height (H_f , sum of highest peak and deepest trough in metres) and peak wave period (T_p), the wave period with the highest energy (given in seconds). During the monitoring period, significant wave height ranged from 1.3 to 9.3 m (mean 3.2, SD 1.3), extreme wave height ranged from 2.1 to 14.73 m (mean 5.6, SD 2.2) and wave period varied from 8.2 to 16.0 s (mean 12.2, SD 1.6).

Weather data for Mercury Island was recorded daily by the staff stationed on the island for the period 1 January 2004 to 6 May 2007. Air temperature ($^{\circ}\text{C}$) was measured three times a day at 0800, 1200 and 1800 hours. Cloud cover (in octaves), wind speed (Beaufort wind force scale) and swell height (m) were estimated by visual observation (at 0800, 1200 and 1800 hours) while water temperature ($^{\circ}\text{C}$) was measured once a day at 0800 hours from the sea adjacent to the MJ.

Data analysis

The proportion of chicks fledged per breeding attempt, the proportion of successful attempts fledging one, two and three chicks and the average brood size in successful attempts were determined for all breeding attempts with a known outcome that were monitored from any point during

incubation. Because nests were not monitored from the onset of egg laying, breeding success has been overestimated. The hatching–fledging interval was estimated for all breeding attempts that were monitored from a point during incubation until the chicks were observed to have left the nest. The estimates are necessarily of low precision because monitoring visits were usually at least 7 days apart and the hatching event could not be observed or reliably estimated in all cases.

To account for the bias introduced by not monitoring all clutches from the start of incubation, nest success was determined using a combination of the Mayfield (1961, 1975) method and parametric survival analysis. This extension of the Mayfield method allows explanatory variables to be incorporated into nest success modelling and makes it possible to use standard approaches (e.g. AIC) to select between models (e.g. Wolfaardt et al. 2008; Zador et al. 2009). As Bank Cormorants are easily disturbed and displaced from their nests (Crawford and Cooper 2005), it was not always possible to record the number of eggs present on every check. Consequently, nest days (rather than egg and chick days) were calculated by taking the mid-point between nest visits (Mayfield 1961) and partial failures were ignored by the model. The mid-point approach is considered to be valid where target visit intervals are under 15 days (Johnson 1979; Crick et al. 2003). Where the laying date was known, but the hatching date could not be reliably estimated, the nest days estimate was constrained to be not greatly longer than the mean laying–hatching interval (30 days; Cooper 1987).

Failure rates were generated and compared using the survreg function in R v.2.10.1 (R Development Core Team 2009) with nest days as the response variable. An exponential error distribution was employed to estimate the survival distribution as this assumes that nests fail at random through time (Zador et al. 2009). Data were considered right censored if the nest persisted through the end of the study period. The maximum likelihood estimate of risk of failure (F) per sampling interval for nests with eggs and chicks was defined as:

$$F = \exp(-\alpha - \beta x) \quad (1)$$

where α and β are the estimated parameters from the regression (intercept and coefficients) and x is the value of the explanatory variable (fixed as $x = 1$ for factorial variables). Using the exponential distribution nest survival (S) at time t was, therefore, defined as:

$$S(t) = \exp(-Ft) \quad (2)$$

As daily mortality rates are likely to differ for different nesting stages, the incubation and chick-rearing periods were considered separately and the survival rate for the whole breeding attempt was derived from the product of

the two. A period of $t = 30$ days (Cooper 1987) was used for hatching success while nest survival during chick-rearing is given for a period of $t = 55$ days. The nestling period has not been well studied, but the species account in Crawford and Cooper (2005) gives a range of 55–70 days based on 16 nests. Approximate upper and lower 95% confidence intervals (CI) for nest survival are given by $\exp[-t(F - 1.96 F/\sqrt{n})]$ and $\exp[-t(F + 1.96 F/\sqrt{n})]$, respectively, where n is the number of failures occurring during either incubation or brooding.

The island and year (e.g. Robben Island 2007), the clutch status (1st or 2nd) and the estimated laying date (ELD) were included in the survival models as explanatory variables. The ELD was taken as (1) the laying date estimated from the standard Mayfield approach, (2) the estimated hatching date minus 30 days (the mean laying–hatching interval; Cooper 1987) or, for nine nests that contained eggs at the first visit but where the eggs did not hatch, (3) the mid-point of the earliest and latest possible laying dates based on Crick et al. (2003). The ELD was incorporated into the model as a sinusoidal curve (as described, for example, by Underhill et al. 1992). The date was converted into an angle from 0° to 360° using 1 January of each year as day one (the choice of date is arbitrary). Differential survival in the various subcolonies was considered separately, as nests were not monitored at all subcolonies in all years. AICc was used to compare model fits.

Nest failure events at Robben Island and at Mercury Island (in 2004/05 only) were related to sea-state and weather data using multiple regression with a binomial error distribution and a logit link function, specified using the glm function in R v.2.10.1 (R Development Core Team 2009). The response variable was the proportion of previously active nests that failed during each visit interval and the explanatory variables were either the mean or the single maximum value occurring in the visit interval from each of the weather and sea-state variables.

A combination of the nest visit data and the active nest counts data (2007 and 2009 only) were used to generate monthly values for the proportion of all active nests that contained eggs (or incubating adults) or chicks for Robben Island in all 3 years. When more than one proportion could be generated for a month (most cases), a mean of all available counts was used as the monthly value. These data were used to determine the peak of breeding activity at Robben Island.

Results

We monitored 337 breeding attempts during incubation (from 285 nests) at a mean (\pm SD) visit interval of 7.5

(± 3.0) days (Table 1). The mean (\pm SD) nest days estimate during incubation was 28.3 (± 14.5) days, including breeding attempts which failed during incubation, and the total number of nest days for which we monitored nests during incubation (9,522.5 days) was 94% of the total number of nest days that would be expected based on 337 breeding attempts and a 30-day laying–hatching interval (10,110 days). Of these 337 breeding attempts, 210 could be followed during the brood period (Table 1).

Age at fledging and breeding success

Of the 210 breeding attempts in which at least one egg hatched, 98 were monitored until the chicks fledged, 84 at Mercury Island and 14 at Robben Island. The mean (\pm SD) hatching–fledging interval from all 98 nests was 57 (± 9) days (95% CI of the mean: 55–59 days). At Mercury Island, 84 nests produced a mean hatching–fledging interval of 57 (± 9) days (95% CI: 55–59), while the mean estimated fledging age at Robben Island was 55 (± 8) days (95% CI: 51–60). The means did not differ significantly (two-sample *t* test: $t = 0.79$; $df = 19.22$; $P = 0.44$).

A total of 156 chicks fledged from the 98 breeding attempts, at a mean brood size of 1.6 (± 0.6) chicks. One chick fledged from 44.9% of the breeding attempts, two chicks fledged from 51.0% and three chicks fledged from 4.1% of the breeding attempts (three at Mercury Island and one at Robben Island). The ratios did not differ between the two colonies (Fisher's exact test: $P = 0.76$). If the 242 breeding attempts monitored from incubation to a conclusion are considered, then 156 chicks equates to 0.64 fledglings/breeding attempt, with the majority (85%) fledging from nests at Mercury Island and 74% of the chicks from Robben Island fledging in 2008 (Table 1).

Nest survival

The overall daily nest failure rate (SD) was 0.011 (0.0011) failures per day during incubation and 0.0039 (0.0007) failures per day during the nestling period (Table 3). These failure rates give a hatching probability of 0.71 (95% CI: 0.67–0.76) and a fledging probability 0.81 (95% CI: 0.75–0.86). The probability that a nest fledged at least one chick was thus 0.57 (95% CI: 0.50–0.65). However, the failure rates and derived survival probabilities were variable both between the two islands (Fig. 2) and between the three breeding seasons at both Robben and Mercury Island (Table 3). Nests had a 21.6% greater survival rate at Mercury than at Robben Island over the whole breeding attempt (Fig. 2), with a more pronounced difference during incubation (18.0%) than during the brood period (11.2%). In addition, survival was better during the brood period than during incubation at both sites (Table 3).

Modelled probabilities of a nest surviving the incubation period ranged from 0.54 (95% CI: 0.41–0.70) at Robben Island during 2009 to 0.84 (95% CI: 0.77–0.91) at Mercury Island in 2009/10, a difference of 30% (Table 3). Survival rates during incubation were 18% higher at Mercury Island than at Robben Island (Model 4A, Table 2: coefficient estimate = -0.70 , $z = -3.7$, $P < 0.001$; Fig. 2), but the strong support for the model considering each year separately (Model 2A, Table 2) indicated that incubation success also varied between years at the two sites. For example, the worst year at Robben Island (2009) differed significantly from Mercury Island in 2004/05 (coefficient estimate = 0.79, $z = 2.6$, $P = 0.008$), 2007/08 (coefficient estimate = 0.79, $z = 2.3$, $P = 0.019$) and 2009/10 (coefficient estimate = 1.38, $z = 4.2$, $P < 0.001$). Survival of nests containing 1st and 2nd clutches did not differ

Table 1 Numbers of breeding attempts monitored during the incubation and brood periods, total numbers monitored to completion (to failure or fledging), monitoring visit intervals and numbers of chicks

Colony and season	No. monitored in incubation	No. monitored in brooding	No. nest visits	Mean (SD) visit interval (days)	No. monitored to completion	No. chicks fledged (per attempt)
Mercury (all seasons)	224	161	52	7.0 (1.9)	165	133 (0.81)
2004/05	95	68	14	6.9 (2.1)	74	52 (0.70)
2007/08	46	30	19	7.4 (1.7)	34	32 (0.94)
2009/10	83	63	19	7.0 (0.0)	57	49 (0.86)
Robben (all seasons)	113	49	52	9.1 (4.7)	77	23 (0.30)
2007	35	15	12	13.7 (5.9)	16	2 (0.13)
2008	34	17	15	7.4 (4.6)	28	17 (0.61)
2009	44	17	25	8.0 (2.4)	33	4 (0.12)
Total	337	210	104	7.5 (3.0)	242	156 (0.64)

The values for chicks fledged per attempt are as a proportion of all breeding attempts monitored to completion

fledging for all Bank Cormorant *Phalacrocorax neglectus* breeding attempts monitored at Robben and Mercury Islands, by total per colony and by breeding season at each colony

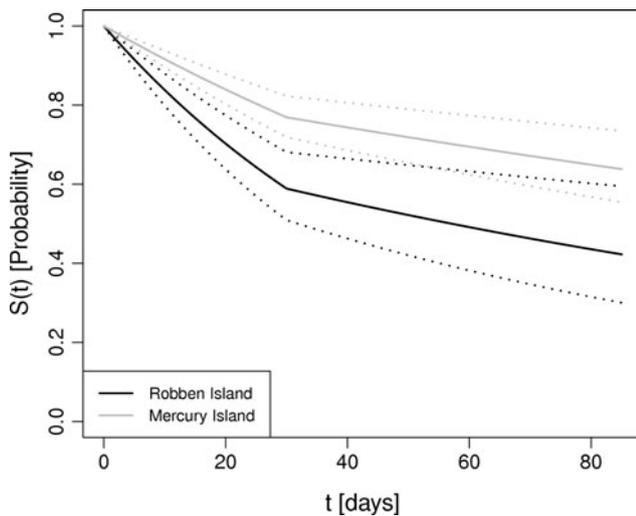


Fig. 2 Bank Cormorant nest survival (probability) over time at Robben (*black*) and Mercury (*grey*) Islands during the whole breeding attempt, based on a 30-day incubation period and a 55-day brood period. The *dotted lines* show the upper and lower 95% confidence limits of the survival probability

significantly during incubation (coefficient estimate = 0.51, $z = 1.8$, $P = 0.08$).

The modelled probability of a nest surviving the chick-rearing period also varied with site and year, ranging from 0.51 (95% CI: 0.30–0.87) at Robben Island in 2009 to 0.96 (95% CI: 0.90–1.00) at Mercury Island in 2007/08, a difference of 45%. However, survival during the brood period seems to have been particularly poor at Robben Island in 2009, as the next lowest survival probability was 23% higher (Mercury Island 2007/08; Table 3). With Robben Island 2009 set as the baseline for the model (Model 3B, Table 2), the probability of a nest surviving the brood

period was significantly higher at Mercury Island in 2007/08 (coefficient estimate = 2.90, $z = 2.7$, $P = 0.007$) and in 2009/10 (coefficient estimate = 1.46, $z = 2.8$, $P = 0.006$). The difference (of 35%) between brood survival at Robben Island in 2008 and 2009 just failed to reach significance ($P = 0.06$) and none of the other differences tested were significant ($P > 0.05$).

Factors contributing to nest failure at Robben Island

Nest survival at the OJ and LA did not differ significantly during either incubation (coefficient estimate = -0.04, $z = -0.10$, $P = 0.921$) or the nestling period (coefficient estimate = 0.17, $z = 0.18$, $P = 0.854$). Subsequently, the data were combined for the analysis relating nest failures to sea-state and weather data.

Nest failures occurring between the monitoring visits at Robben Island were positively related to both the extreme wave height (coefficient estimate = 0.20, $z = 3.8$, $P < 0.001$) occurring at sea and the mean of the daily maximum temperatures (coefficient estimate = 0.17, $z = 2.5$, $P = 0.012$) during the visit intervals (Model 6A, Table 4). The model containing the interaction term was not well supported and the interaction was not significant ($P > 0.05$).

Monthly active nests counts (including those that were empty) peaked in July in both 2007 and 2009 (Fig. 3, top panel), while the proportion of all active nests that had contents (eggs or chicks) in each month peaked in June in 2007 and 2008 but only in September in 2009 (Fig. 3, bottom panel). The two counts together suggest that May–July represents the period of peak breeding activity at Robben Island in most years. In 2007 and 2009, the major storm events of the year occurred during this period, while

Table 2 Model selection for survreg models used to explain nest survival during the incubation and brood periods at Robben and Mercury Islands

Model no.	Model	K	AICc	ΔAICc	AICc weight
Incubation period					
2A	Island and year + Clutch status	7	1,183.35	0.00	0.39
4A	Island	2	1,183.59	0.24	0.34
3A	Island and year	6	1,184.64	1.30	0.20
1A	Island and year + Clutch status + Sine(LD) + Cosine(LD)	9	1,186.78	3.44	0.07
5A	Intercept only	1	1,194.49	11.14	0.001
Brood period					
3B	Island and year	6	468.90	0.00	0.57
2B	Island and year + Clutch status	7	471.04	2.14	0.20
4B	Island	2	472.78	3.87	0.08
1B	Island and year + Clutch status + Sine(LD) + Cosine(LD)	9	472.92	4.01	0.08
5B	Intercept only	1	473.06	4.16	0.07

Models 1A and 1B include two terms, Sine(LD) and Cosine(LD), which fit the estimated laying date as a sinusoidal curve to include the effect of seasonality as a continuous explanatory variable (Underhill et al. 1992). Model selection is based on AICc weights. K is the number of parameters in each model and $AICc$ values are derived from a sample size of 337 for incubation and 210 during the brood period

Table 3 Modelled daily failure rates, nest survival probabilities and 95% confidence intervals (CI) for each breeding season at Robben and Mercury Islands

	Mercury Island			Robben Island		
	2004/05	2007/08	2009/10	2007	2008	2009
Incubation (30 days)						
No. nest failures	26	15	17	12	17	22
Total nest days	2,302	1,429	2,901.5	934	899	1,057
Daily failure rate	0.011	0.011	0.006	0.013	0.019	0.021
(SD)	(0.002)	(0.003)	(0.001)	(0.004)	(0.005)	(0.004)
Survival probability	0.71	0.73	0.84	0.68	0.57	0.54
95% CI	0.63–0.81	0.62–0.86	0.77–0.91	0.55–0.85	0.43–0.74	0.41–0.70
Brood (55 days)						
No. brood failures	15	1	9	3	2	6
Total nest days	2,735.5	1,473	3,156.5	605.5	730	488.5
Daily failure rate	0.006	0.0007	0.003	0.005	0.003	0.012
(SD)	(0.001)	(0.0007)	(0.001)	(0.003)	(0.002)	(0.005)
Survival probability	0.74	0.96	0.86	0.76	0.86	0.51
95% CI	0.64–0.86	0.90–1.00	0.772–0.95	0.56–1.00	0.70–1.00	0.30–0.87
Overall (85 days)						
Survival probability	0.53	0.70	0.72	0.52	0.49	0.27
95% CI	0.40–0.70	0.56–0.89	0.60–0.86	0.31–0.88	0.302–0.79	0.12–0.61

Survival probabilities are based on a 30-day incubation period and a 55-day chick-rearing period. Overall survival probabilities are the product of the incubation and brood period

Table 4 Model selection for generalised liner models used to explain nest failures occurring during monitoring visit intervals at Robben Island 2007–2009 and at Mercury Island 2004/05

Model No.	Model	K	AICc	ΔAICc	AICc weight
Robben Island 2007–2009					
6A	EW + MMaxT	3	136.96	0.00	0.38
5A	R + EW + MMaxT	4	137.50	0.54	0.29
9A	EW*MMaxT	4	139.41	2.45	0.11
4A	R + EW + MAW + MMaxT	5	139.49	2.53	0.11
Mercury Island 2004/05					
5A	MaxT + MaxW	5	75.39	0.00	0.55
8A	MaxT	4	77.94	2.55	0.15
4A	MaxT + MaxS + MaxW	6	78.61	3.22	0.10
6A	MaxT*MaxW	6	78.99	3.60	0.09

Explanatory variable codes: *R* rainfall; *EW* extreme wave height, *MAW* maximum of the daily average wind speed, *MMaxT* mean of the daily maximum temperatures, *MaxT* maximum temperature occurring in the visit interval, *MaxS* maximum swell height occurring in the visit interval, *MaxW* maximum wind speed occurring in the visit interval. *K* is the number of parameters in each model and *AICc* values are based on a sample size of 43 (visit intervals) for Robben Island and 24 for Mercury Island. + fits main effects only and * fits interactions and main effects. Only the top four models (based on *AICc* weights) are shown in each case

in 2008, the largest storm events occurred in August and September (Fig. 4a, c, e), after many of the birds had finished breeding. An examination of the daily values for extreme wave height indicated that the most severe event of the year in 2007 occurred on 27 July (15.5 m), towards the end of nest monitoring, while in 2008, the major storm events, on 31 August (14.6 m) and 1

September (14.4 m), actually fell outside the nest monitoring period altogether (Fig. 4c, d). In contrast, large storm events that coincided with high levels of breeding activity, such as the c. 12 m storm on 17 May 2008 or the c. 15 m storm on 23 and 24 June 2009, were associated with fairly widespread failure events (up to 71% of nests active at the previous visit).

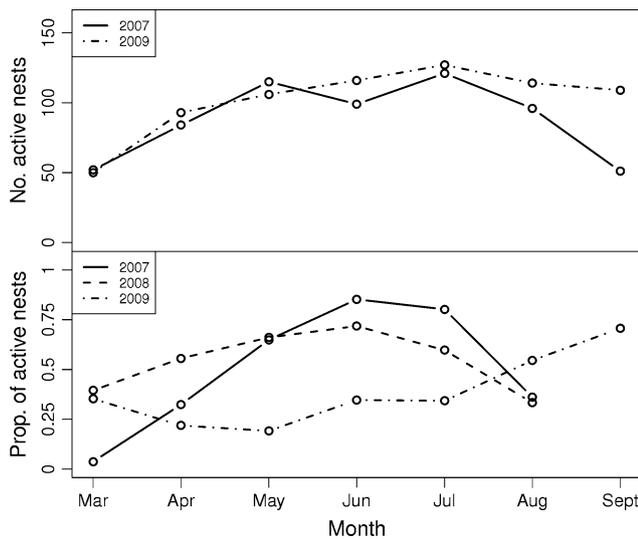


Fig. 3 Top panel counts of active nests of Bank Cormorants in each month from March to September at Robben Island in 2007 (solid line) and 2009 (dashed and dotted line). Bottom panel breeding activity of Bank Cormorants by month during the study period, shown as the proportion of nests counted as active (being built, empty but with adult(s) present, with nest contents) that contained eggs or chicks, at Robben Island in 2007 (solid line), 2008 (dashed line) and 2009 (dashed-dotted line)

In the 2 years when the largest storms occurred later in the season (relative to 2009), the proportion of the active nests in the study that were either incubating eggs or brooding chicks each month peaked in May (0.52) and June (0.47), respectively, in 2007, and in April (0.56) and July (0.48), respectively, in 2008 (Fig. 4b, d, f). In 2009, the peak in the proportion incubating (0.46) only occurred in August, while the brooding proportion only surpassed 0.1 in September (Fig. 4f), just before monitoring was terminated. This suggests that the majority of eggs would hatch in May or June when breeding is not interrupted by storm events. This was supported by the mean hatching dates in study nests containing 1st clutches of 22 May 2007, 25 May 2008 and 1 May 2009, respectively.

Finally, the significant effect of temperature appeared to be driven by periods where the mean of the daily maximum temperatures remained above 20°C for a few monitoring visits. Eleven nest attempts failed in two such periods in March and April of both 2007 and 2009. Seven of these nests contained eggs and four contained chicks. These periods were also characterised by days where the single highest maximum temperature recorded exceeded 25°C.

Factors contributing to nest failure at Mercury Island

Survival did not differ significantly between the MJ and four of the other subcolonies (BR, GR, EB, OMJ) sampled in 2004/05 during either incubation or brooding (all

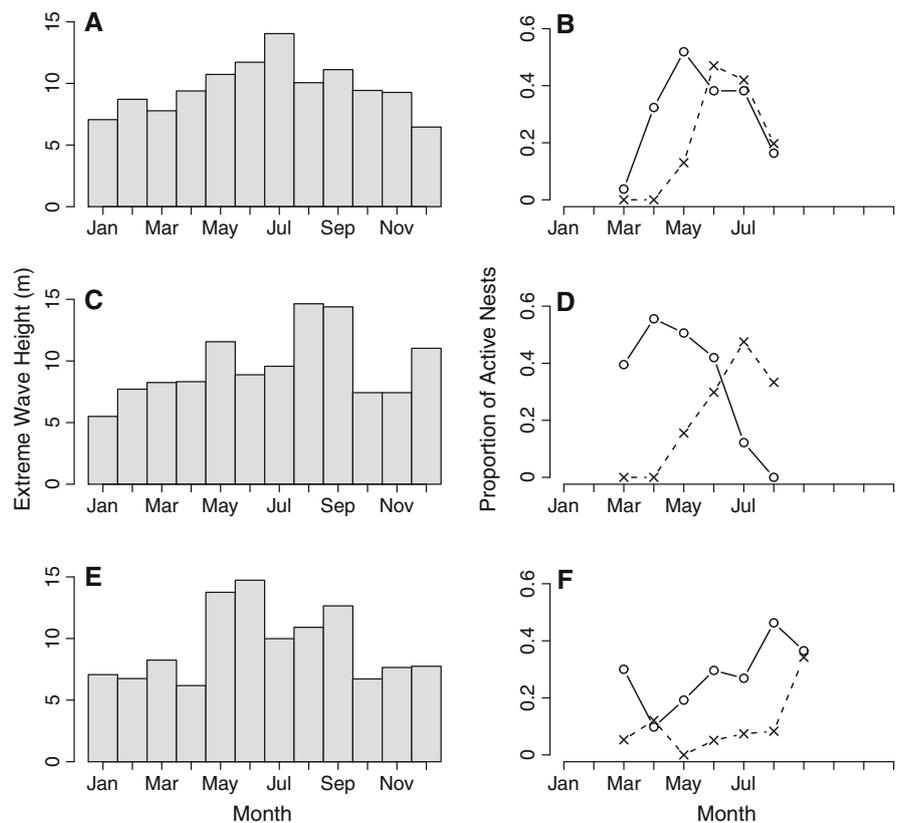
P values > 0.05). The remaining subcolony (TR) had significantly lower modelled nest survival probabilities than the MJ for both the incubation (0.54 vs. 0.90; coefficient estimate = -1.74, *z* = -2.1, *P* = 0.037) and chick-rearing periods (0.24 vs. 0.84; coefficient estimate = -2.14, *z* = -2.6, *P* = 0.009). In 2009/10, the modelled nest survival probabilities were higher for both incubation and brooding at the MJ than at the two additional subcolonies (OMJ and TR), but these differences were not significant (all *P* values > 0.05). In the 3 years, the survival probabilities over the whole breeding attempt for nests on the MJ only varied from 0.70 in 2007/08 (95% CI: 0.56–0.89) to 0.76 (95% CI: 0.63–0.90) in 2004/05.

The timings of the 26 nest failures which occurred during incubation at Mercury Island in 2004/05 were not significantly related to any of the weather or sea-state variables measured during the monitoring period (*P* values from all models > 0.05). In contrast, the proportion of nest attempts that failed between visits in the chick-rearing period was significantly related to the maximum temperature occurring in the visit interval (coefficient estimate = 0.67, *z* = 3.4, *P* < 0.001), while the combined failure proportion (incubation and brooding) showed a significant positive relationship with the maximum temperature (coefficient estimate = 0.34, *z* = 2.8, *P* = 0.005) and a significant negative relationship with the maximum wind speed occurred in the visit interval (coefficient estimate = -0.29, *z* = -2.4, *P* = 0.018; Model 5A, Table 4). One visit interval (18–24 January) accounted for 42% of the incubation failures that occurred during the season (*n* = 26) and, although it was characterised by average maximum temperatures, the maximum wind speed estimate never exceeded 4 on the Beaufort scale and was 2 or less on 4 of the 7 days. Two visit intervals in February (2–7 February and 15–17 February 2005) accounted for two-thirds of the brooding failures (*n* = 15), while two additional failures occurred in the interval separating them (8–14 February 2005). These visit intervals contained the two highest daily maximum temperatures recorded in the 2004/05 monitoring period and the two highest temperatures recorded during February between 2004 and 2007.

Discussion

Prior to this study, the only data available on the breeding success of Bank Cormorants suggested an overall hatching success of 52.5% and fledging success of 61.4% based on individual chicks and eggs (unpublished data from Cooper, cited in Crawford and Cooper 2005). The 10% difference between the survival probabilities for incubation (0.71) and the brood period (0.81) from the Robben and Mercury Island data combined matches well to the difference

Fig. 4 *Left* maximum values for extreme wave height (H_T) recorded at Cape Point, South Africa, in each month of the year for 2007 (a), 2008 (c) and 2009 (e); *Right* breeding activity of Bank Cormorants by month during the study period, shown as the proportion of nests deemed to be active (being built, empty but with adult(s) present, with nest contents) that contained either eggs (circles and solid line) or chicks (crosses and dashed line), at Robben Island in 2007 (b), 2008 (d) and 2009 (f)



between hatching and fledging success reported by Crawford and Cooper (2005). In addition, although the breeding success estimate obtained in this study (0.64 fledglings/breeding attempt) was an overestimate, it is also similar to the value of 0.63 fledglings/breeding attempt given by Crawford and Cooper (2005). Our estimate is unlikely to have been greatly inflated, as the majority of the incubation period was monitored. However, the breeding success of the Bank Cormorants in this study differed markedly between the two sites (Table 1) as, to a lesser extent, did the probability of nests surviving the breeding attempt, both between sites and between seasons (e.g. differences between incubation and brooding survival at Mercury Island of 16% in 2009/10 and 23% in 2007/08).

Variability in breeding success between years is commonly reported in seabirds (Furness and Monaghan 1987; Hamer et al. 2001), including cormorants (Aebischer and Wanless 1992). This variability can be influenced by disease (Weimerskirch 2004), parasite loads (Duffy 1983), predation (Wanless et al. 2007), human disturbance (Anderson and Keith 1980) or altered prey quality and availability following changes in oceanographic conditions (e.g. Wanless et al. 2005). Changes in diet composition have been implicated in declines in breeding success of cormorants (Aebischer and Wanless 1992; Crawford et al. 2003), and alterations in food availability are believed to

pose a significant risk to a number of seabird species in the Benguela ecosystem (Kemper et al. 2007; Crawford et al. 2008b), including Bank Cormorants (Crawford et al. 2008a). It is possible that food availability could have influenced nest survival in this study. In particular, 2009 may have been a poor year for food availability at Robben Island; dead medium-sized chicks were observed in three nests in 2009 and were not seen in other years, while the probability of chicks surviving to fledging was more than 20% higher in the other two seasons. However, the diet and foraging ecology of Bank Cormorants in South Africa is poorly studied (but see Cooper 1985; Crawford and Cooper 2005) and a long-term dataset to investigate the extent of interannual variation is required. Without diet samples or information on foraging behaviour (which could not be obtained during 2007–2009), the possibility that altered feeding conditions contributed to the reduced nesting success at Robben Island cannot be ruled out.

Variability in breeding productivity is often pronounced in species inhabiting eastern boundary current systems, such as the Benguela ecosystem. For example, breeding success of Brandt's Cormorant *P. penicillatus*, an endemic to the California current, ranged from 0 to 2.6 chicks fledged/pair between 1983 and 1993 (Nur and Sydeman 1999). In contrast, apart from at the TR sub-colony in 2004/05, where the failures that occurred during

chick-rearing appeared to be related to heat exposure, the variation in nest success was relatively low at Mercury Island between years, particularly at the MJ (a maximum of 6% difference). Bearded Goby seems to be an abundant and reliable food source around Mercury Island (Ludynia et al. 2010a), where it also dominates the diet of breeding African Penguins *Spheniscus demersus* (Ludynia et al. 2010b). A reliable food source could explain the low variability in chick survival observed between seasons at Mercury Island's MJ. However, the inability to detect significant differences between the sub-colonies or seasons could have resulted from small sample sizes, particularly during the chick-rearing period; for example, Klett and Johnson (1982) have suggested a minimum of 50 nests should be used for comparisons with the Mayfield method.

Although it may be predictable in its distribution at Mercury Island (Ludynia et al. 2010a), Bearded Goby is considered to be of relatively low energetic content (Ludynia et al. 2010b). Reliance on low-energy food, even if that food is abundant or easy to obtain (the junk-food hypothesis, e.g. Osterblom et al. 2008), can affect breeding success (e.g. Wanless et al. 2005). Bank Cormorants in this study only raised 0.63 fledglings/breeding attempt and produced a maximum of 0.97 fledglings/pair at Mercury Island (in 2007/08). These are relatively low outputs compared to other benthic foraging, marine congeners or those of a similar size to the Bank Cormorant. Studies have suggested that the Brandt's Cormorant averages around 1.5 (max. 2.6) fledglings/pair (e.g. Boekelheide and Ainley 1989; Nur and Sydeman 1999; Jones et al. 2008), species in the Blue-eyed Shag complex *P. atriceps* around 1.0–1.9 fledglings/pair (e.g. Brothers 1985), the European Shag *P. aristotelis* 1.2–1.9 fledglings/pair (e.g. Snow 1960; Aebischer and Wanless 1992), the Large Pied Cormorant *P. varius* 1.4–1.5 fledglings/pair (Powlesland et al. 2008) and the Little Pied Cormorant *P. melanoleucos* 1.3–1.6 fledglings/pair (Taylor 1987; Powlesland and Luke 2000). Poor energy content in the diet may in part explain the poor reproductive output noted in this study, but this needs to be investigated further.

Besides responding to variability in long-term changes in oceanographic conditions, breeding success can also be influenced by small-scale atmospheric perturbations (see Schreiber 2001 for a review). In general, seabirds are relatively unaffected by normal weather patterns (Schreiber 2001). However, unusual or extreme weather events can affect breeding success either indirectly, for example by reducing food availability or increasing the costs associated with finding food (Finney et al. 1999), or else directly by causing egg or chick mortality (Seddon and van Heezik 1991). For example, a gale destroyed 49% of 761 European Shag nests on the Isle of May, Scotland, in 1982

(Aebischer and Wanless 1992), causing a 31% reduction in the number of chicks fledged/pair (Aebischer 1999).

A direct effect of weather events on chick and egg mortality seems to be the most likely cause for the years of lower nest survival in this study. At Robben Island, nest failures were related to the height of storm waves, and at some of the smaller subcolonies at Mercury Island in 2004/05, a few days of high air temperatures, coupled with little to no wind, seem to have been responsible for heightened chick mortality. Exactly what drives Bank Cormorants to breed during summer in Namibia has not been studied, but the prevailing southerly winds during this period intensify the coastal upwelling in the central and southern parts of the Northern Benguela system (Roux 2003). These onshore winds also appear to have a cooling effect on the offshore islands, and it is probably their influence on ambient temperatures at the surface (e.g. Frost et al. 1976) that allows thousands of seabirds to nest in the open during the austral summer in Namibia. This idea is supported by the fact that the largest failure event during incubation on Mercury Island in 2004/05 occurred in a period of average temperatures, but low maximum wind scores. Heat-stressed African Penguins will abandon their nests to go to sea to cool down, leaving eggs vulnerable to predation by Kelp Gulls *Larus dominicanus* (Frost et al. 1976; Randall 1983). Kelp Gulls are known to take Bank Cormorant eggs if adults leave the nest unguarded (Cooper 1987), and this mechanism could explain the egg losses observed at Mercury Island in 2004/05.

Bank Cormorants, because of their habit of nesting close to the water (Cooper 1986), may also be particularly susceptible to the impact of storm waves; although nest losses to waves have also been recorded in Blue-eyed Shags, Little Pied Cormorants and Crowned Cormorants *P. coronatus* (Brothers 1985; Taylor 1987; J.K., personal observation). The situation could potentially be exacerbated at Robben Island by the nesting areas used there. Nests on the OJ are c. 4 m above the water and many nests on the harbour wall are built <2 m from the water at high tide (R.B.S., personal observation). During large storms, particularly those with north-westerly winds, large waves frequently wash right over the OJ and occasionally the LA of the harbour (R.B.S., personal observation). Birds on both structures would be at risk of losing nest contents in these extreme events, particularly during incubation or the early stages of chick-rearing. Eggs could easily be washed from nests and small chicks would also be at risk of being washed away, drowning, or succumbing to hypothermia if the nest was drenched (e.g. Konawzewski and Taylor 1989; Seddon and van Heezik 1991). Small chicks may also suffer more readily from indirect effects of extreme climate events, if, for example, foraging becomes more difficult for their parents (e.g. Finney et al. 1999). Medium to large

chicks may be able to better withstand storm events and, once old enough, may even be able to climb back to their nest if washed out. This has been observed once at the OJ (R.B.S., personal observation).

From this perspective, the timing or frequency of extreme storm events may be just as important as their severity with respect to their impact on breeding success (Aebischer and Wanless 1992; Frederiksen et al. 2008). In all 3 years studied, the most extreme storm events (measured by wave height) occurred during May–September (Fig. 4), the period of peak breeding activity for Bank Cormorants in the Western Cape (Crawford et al. 1999; Figs. 3 and 4). Although there was parity between the years in terms of the severity of the storm events (4 months containing maximum waves >10 m and extreme values of c. 15 m), there were clear differences in the timing of storms and, in particular, the extreme storm events (Fig. 4). In 2007, the maximum wave values were recorded at the end of July, by which time most nests contained large chicks and the storm did not cause any failures. Similarly, in 2008, the extreme storm events were in late August and September, outside the monitoring period. However, the smaller storm in May occurred when a lot of birds were incubating and caused 7 nest failures on the OJ, leading to the relatively low nest survival during incubation in that year. This storm may also explain the lag between the peak in the proportion of nests incubating and brooding in 2008, as some pairs may have produced replacement clutches. In contrast, in 2009, the two largest storm events of the year occurred in the middle of the period of peak breeding activity at Robben Island (Fig. 4e). In particular, the storm in June, the most severe recorded during the study, coincided with high levels of activity in the study nests and caused 10 nests (71%) to fail, 9 of which contained eggs prior to the storm event and 1 which contained small chicks. To what extent these storm events influence the breeding phenology (e.g. result in the elongated breeding season) in South Africa is not clear. It was a shortcoming of this study that birds were not individually marked with field-readable rings and this limited our ability to draw inferences on the responses of individuals and pairs to failure events or nest losses.

Although the storm in May 2009 did not cause any direct failures, it did remove five nests that were in the process of being built on the OJ, probably contributing to the eventual abandonment of that site for the year. Bank Cormorants spend 24–44 days nest building before laying the first egg and mainly obtain nest material by diving (Cooper 1986). A complete Bank Cormorant nest may represent around 240 diving bouts and 18 h of investment (Cooper 1986). This is a relatively energetically expensive way of obtaining nesting material; diving can cost around 5–10 times the basal metabolic rate in energy expenditure

in cormorants (see table 1 in Enstipp et al. 2005), possibly more in cold water (Enstipp et al. 2007) as cormorants have a partially wettable plumage and, unlike some other divers, little subcutaneous fat (Grémillet et al. 2005). Consequently cormorants try to minimise the time they spend in the water to balance their energy budget (e.g. Grémillet et al. 2001). The majority of nest building occurs prior to egg laying in Bank Cormorants (Cooper 1986), thus having to replace a complete (or even partially built) but empty nest may represent a serious energetic cost to a breeding pair. This remains to be investigated, but, if it is so, losing empty nests could potentially reduce the likelihood of any subsequent breeding attempts ending positively.

In many circumstances, man-made structures seem to provide adequate nesting habitat for the Bank Cormorant, or even allow breeding to occur where it otherwise could not. The nests on the MJ on Mercury Island showed some of the highest survival probabilities in this study, with low variability between seasons. In 2004/05, when both nests built on man-made and natural substrates were monitored, nests on the MJ and OMJ had the highest probability of survival, probably as these man-made structures provided shelter from the sun in what appeared to be an unusually warm season. However, the high failure rates recorded in nests from the OJ and LA at Robben Island suggest that at least some of the population there may be restricted to utilising suboptimal nesting sites. The SA, the only other breeding site on Robben Island, can hold up to 90 nests at the height of the season and these seem to be built only within an area that approximately correspond to the extent of shelter from wave action provided by the LA. Basic observations and counts of nests on the SA suggest that most suitable sites are occupied at the height of breeding activity (R.B.S., personal observation). Birds may thus be restricted to breeding on the OJ and LA either because other suitable nesting habitat is absent at Robben Island or because the presence of human activity and terrestrial predators (e.g. Feral Cats *Felis catus*; Braby and Underhill 2007) precludes ground-nesting (as occurs at, e.g., Mercury Island). The Stony Point colony, in the Western Cape, was occupied by Bank (and other) Cormorants within a few months of its permanent protection from disturbance (Cooper 1988), while the arrival of terrestrial predators following the connection of Bird Island, Lambert's Bay, to the mainland via a causeway may have contributed to the demise of the colony there (du Toit et al. 2003).

Understanding whether extreme, stochastic weather events, can impose limits on the Bank Cormorant population (in the sense of Frederiksen et al. 2008) may prove to be crucial for the continuing survival of the colony at Robben Island, and perhaps the survival of the species. Under most future climate change scenarios, environmental variability is expected to increase, extreme events are

anticipated to occur with greater frequency or intensity (e.g. Mason et al. 1999 and references therein; Roux 2003) and southern Africa is expected to warm (New et al. 2006). Extreme weather events have been shown to hinder survival and population growth in European Shags (Frederiksen et al. 2008) and Bank Cormorants, thanks in part to their nesting habits (Cooper 1986), may also be vulnerable to similar processes. Increases in spring and summer air temperatures would apply additional pressure at both ends of the breeding season to seabird species breeding on the surface during winter in South Africa and could have an even more pronounced impact in Namibia, where c. 70% of the total Bank Cormorant population breed during summer (Crawford et al. 1999; Kemper et al. 2007). Increased air temperatures, coupled with future changes in summer wind patterns which could occur in southern Namibia (Roux 2003), could potentially cause widespread egg and chick mortality in species nesting on the surface during summer, even in the absence of any associated alterations in upwelling intensity.

Gaining such an understanding will require the continuation of the monitoring programme described here, as well as the expansion of the programme to additional colonies. In addition, studies on the foraging ecology of Bank Cormorants at Robben Island are needed to elucidate whether or not food availability limits that colony. If, except perhaps under extreme circumstances (e.g. during Rock Lobster mass walk-outs; Cockcroft 2001), Bank Cormorants at Robben Island are not limited (at the current population level) by a food-imposed carrying capacity, then a paucity of suitable nesting sites may be imposing a density-dependent control on growth of the population. In this case, the simple addition of an alternative structure, for example a platform within the harbour area, might allow Robben Island to support a larger population of this endangered, endemic seabird.

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