Chapter 19

Trends in numbers of Cape Cormorants (*Phalacrocorax capensis*) over a 50-year period, 1956/57–2006/07

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The population trend of Cape Cormorants (*Phalacrocorax capensis*), a species endemic to southern Africa and that feeds mainly on shoaling pelagic fish, is described for a 50-year period: 1956/57–2006/07. The main breeding localities for the species are grouped in three regions in the Benguela upwelling ecosystem: guano platforms off central Namibia, islands off southern Namibia and islands off South Africa's Western Cape Province. From 1956/57 to 1978/79, the numbers breeding increased off Namibia, as a result of increased availability of breeding space and adequate supplies of food. In the same period, numbers remained stable in the Western Cape. Numbers decreased off southern Namibia in the early 1980s and off central Namibia in the early 1990s, when environmental perturbations reduced the availability of food. Numbers decreased in the Western Cape in the early 1990s, following periods of scarcity of anchovy (*Engraulis encrasicolus*), an important prey item, and an outbreak of avian cholera caused by the bacterium *Pasteurella multocida*. They remained low as cholera outbreaks continued and some pelagic fish were displaced to the east beyond the foraging range of breeding cormorants. The overall population of Cape Cormorants was of the order of 100 000 pairs in 1956/57 and 2005/06, increasing to about 250 000 pairs in the 1970s.

Keywords: Avian cholera, Cape Cormorant, environmental perturbation, food, guano, *Phalacrocorax capensis*, population trend

Introduction

The Cape Cormorant (*Phalacrocorax capensis*) is the most numerous of four cormorants that breed in the Benguela upwelling ecosystem off south-western Africa (Crawford *et al*. 1991). It is endemic to the Benguela ecosystem, where its present breeding range extends from Ilha dos Tigres, southern Angola, to Nelson Mandela Bay, Eastern Cape Province, South Africa (Figure 1; Cooper *et al*. 1982; Dean *et al*. 2002). Its usual non-breeding range is from Lobito, Angola to Delagoa Bay, Moçambique. Vagrant birds have been recorded as far north as Gabon on the West African coast (Hockey *et al*. 2005).

The Cape Cormorant feeds in sub-surface marine waters around the coast by pursuit diving, often in flocks (Rand 1960), sometimes entering lagoons. Its main prey is anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), horse mackerel (*Trachurus trachurus*) and pelagic goby (*Sufflogobius bibarbatus*). It also eats several other fish species and crustaceans (Hockey *et al*. 2005). Together with the Cape Gannet (*Morus capensis*), it is the main producer of seabird guano in southern Africa (Crawford and Shelton 1978). From 1930–1963, four platforms were constructed in northern Namibia to facilitate the collection of guano deposited by Cape Cormorants (Cooper *et al*. 1982).

The Cape Cormorant is regarded as Near Threatened because of a decrease in the breeding population from 277 000 pairs in 1977–1981 (Cooper *et al*. 1982) to about 72 000 pairs in 1996 (Barnes 2000; Simmons and Brown 2007). In order further to investigate trends in the abundance of the species, we collate information on numbers breeding over a 50-year period: 1956/57–2006/07. We consider various factors that may have influenced trends in the numbers of Cape Cormorants, including the availability of food, which may be altered by both fishing and environmental change (Crawford *et al*. 2007), availability of breeding space (Cooper *et al*. 1982), disease (Crawford *et al*. 1992a) and predation (Marks *et al*. 1997), and also compare trends in the populations of Cape Cormorants and Cape Gannets.

Methods

Estimating trends in the abundance of Cape Cormorants is difficult for several reasons. The species has bred at 70 localities and it breeds throughout the year (Hockey *et al*. 2005), although seasons of intensive breeding may be distinguished (Berry 1976; Crawford *et al*. 1999b). Replacement laying may occur after nest failure and successful breeders sometimes relay in same season (Hockey *et al*. 2005). However, breeding may occur in waves, with different birds arriving at colonies at different times (Berry 1976). Therefore, we concentrate on 16 localities, which in 1977–1981 sup-

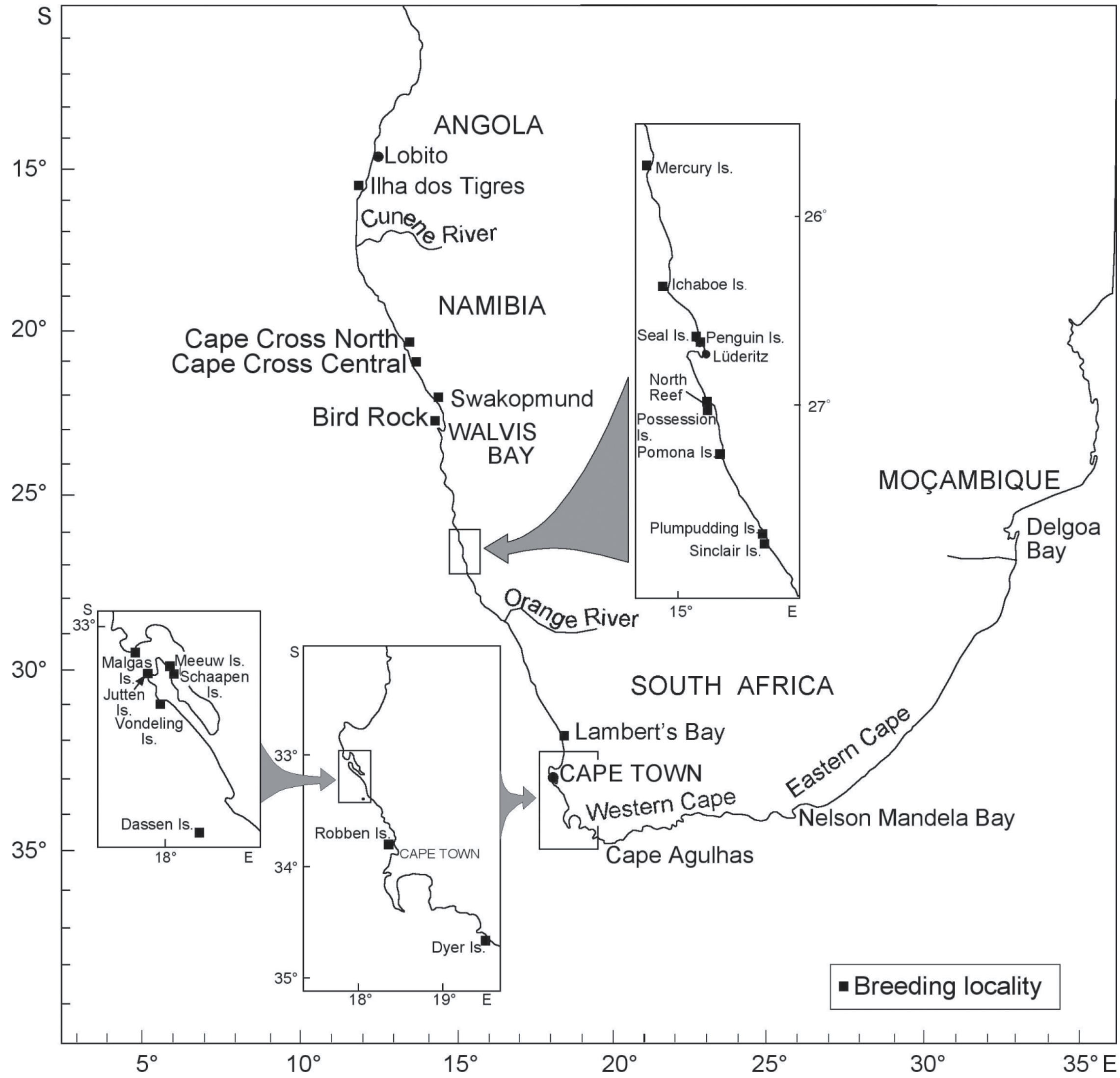

Figure 1: Southern Africa showing the breeding localities of Cape Cormorants and other localities mentioned in the text

ported more than 99% of the overall population (Cooper *et al*. 1982) and have been monitored more consistently than smaller colonies: the four guano platforms (Cape Cross north, Cape Cross central, Swakopmund and Bird Rock) off central Namibia (74 471 pairs or 27% of the population in 1977–1981); Mercury, Ichaboe, Seal (Lüderitz), Penguin (Lüderitz), North Reef and Possession islands off southern Namibia (95 654 pairs; 35%); and Lambert's Bay, Malgas, Jutten, Vondeling, Dassen and Dyer islands off South Africa's Western Cape (104 741 pairs; 38%). We additionally present information for some smaller colonies that were monitored sporadically during the 50-year period. Because of the possibility of absenteeism of breeders at the time counts were conducted, where feasible we have applied a smoothing algorithm to gauge trends from estimates of abundance.

Counts of active nest sites of Cape Cormorants were made on visits to breeding localities. Nest sites were defined as paired birds defending a site, sites showing evidence of recent nest construction, and sites with eggs or chicks. Nests were identified as belonging to Cape Cormorants through identification of birds present at the nests, or using nest characteristics as described in Hockey *et al*. (2005). When unattended chicks were found in crèches away from nests, the number was divided by three to estimate the number of nest sites they represented, as nests at which these chicks were reared would not have been counted. Remainders were taken to represent further sites (Shelton *et al*. 1982). The mean size of clutches is 2.82 eggs (Berry 1976). At breeding localities that were visited frequently, old nests were not counted because of the possibility that birds may breed twice in a season (Hockey *et al*. 2005). At localities that were seldom visited, all nests were counted because old nests are unlikely to remain intact for more than a year due to prevailing strong winds. At Dyer Island, repeat counts of two groups of breeding cormorants were made in 1985 to estimate the coefficient of variation (CV) of the counts.

Photographs, taken vertically from an aeroplane, were often used to estimate numbers at localities where large numbers of Cape Cormorants breed, or which could not be easily accessed. On the photographs, counts were made of cormorant nests, which can be readily distinguished as black spots against a lighter background, whereas individual birds appear as smaller black specks. Generally photographs were taken as close to midday as possible to minimise the effect of shadows. On aerial photographs, the CV on a count of a colony of 3 703 nests was 3.6% (Shelton *et al*. 1982). On photographs of Ichaboe Island, where several species of cormorant nest in mixed colonies, ground-truth information on the abundance of other species of cormorant (e.g. Crawford *et al*. 1999a) was used to adjust counts (Shelton *et al*. 1982). Counts for all localities up until 1981 have been

Table 1: Counts of the number (thousands of pairs) of Cape Cormorants breeding at selected localities, 1956/57 and 1978/79–2006/07

	Cape Cross north	Cape Cross central	Swakopmund	Bird Rock	Mercury Island	Ichaboe Island	Seal Island	Penguin Island	Possession Island	North Reef	Pomona, Plumpudding & Sinclair islands	Lambert's Bay	Malgas Island	Marcus Island	Jutten Island	Schaapen Island	Meeuw Island	Vondeling Island	Dassen Island	Robben Island	Dyer Island
1956/57	0.000	9.426		2.569	1.540	0.353	1.028	0.000	**0.000**		0.005	30.977	14.547	**0.000**	27.757			8.300	11.760	**0.000**	3.186
1978/79	4.944	25.653	43.542	0.332	5.890	21.695	21.457	18.292	**0.083**	1.177	0.096	13.519	8.708	**0.000**	24.277	**0.141**	**0.055**	7.890	13.767	**0.000**	35.580
1979/80						45.805	3.071	**13.000**	**0.300**	0.630		**9.604**	**0.453**			**0.207**	**0.029**			**0.000**	
1980/81					**8.840**	33.700			**0.100**	0.900	0.080	0.969						**3.000**	**22.500**	**0.000**	**16.250**
1981/82						38.636	**2.200**	**1.100**	**1.400**			13.275		**0.005**							
1982/83												1.446									
1983/84												11.573								**0.000**	
1984/85						24.201						2.081								**0.000**	
1985/86					**0.120**	15.232	**0.330**	**5.222**	**6.431**	**0.533**		2.727	**0.021**	**0.000**	**0.217**			**0.002**	**11.144**	**0.002**	**48.293**
1986/87					**0.414**		3.653	**0.321**	**0.286**	**0.521**		8.144			**13.000**	**0.139**	**0.065**			**0.000**	**36.982**
1987/88					**0.088**	6.542		**0.003**	**5.006**	**0.114**		0.936						**0.032**		**0.000**	
1988/89	5.559	0.000	53.420	**0.924**		16.619	**0.000**		**5.592**	**1.268**		**4.413**	**3.067**		**16.466**			0.252	**48.182**	**0.000**	23.355
1989/90						26.781						**2.436**	**0.000**		**2.548**			**0.200**	**0.002**	**0.000**	**3.255**
1990/91										**0.000**		**2.882**	**0.571**	**0.000**	29.819			**15.026**	**3.078**	**0.000**	**8.601**
1991/92						**9.790**						**4.769**	**5.362**	**0.000**	**13.472**	**0.844**	**0.099**	**4.116**	**29.613**	**0.006**	**32.964**
1992/93	0.000	0.000	50.871	3.000	**1.665**	**22.698**	**1.503**	**3.014**	**2.732**	**0.000**		**2.153**	**1.199**	**0.000**	**8.114**	**0.617**	**0.042**	**6.271**	**36.486**	**0.004**	**18.419**
1993/94	0.000	0.000	55.927	0.438	**0.810**	**14.318**	**0.310**	**1.656**				**1.409**	5.481	**0.000**	**10.029**	**0.500**	**0.000**	**0.004**	**0.345**	**0.000**	**18.350**
1994/95	0.000	0.000			0.000	13.000						**0.000**	**0.050**	**0.000**	**0.214**	**0.264**	**0.107**	**10.717**	**0.008**	**0.000**	**14.556**
1995/96					**0.002**	**18.272**	**0.000**	**0.106**	**2.846**	**0.006**	**0.608**	**2.520**	**2.370**	**0.000**	**5.862**	**0.540**	**0.087**	**2.452**	**7.153**	**0.000**	**14.768**
1996/97	0.000	0.000	32.041	8.677	**2.834**	**16.888**						**0.643**	**0.849**	**0.000**	**6.623**	**1.155**	**0.330**	**3.694**	**1.078**	**0.000**	**13.828**
1997/98	1.855	0.131	31.920	1.554	**0.924**	19.745						**0.958**	**3.025**	**0.006**	**5.064**	**0.879**	**0.637**	**4.159**	**0.667**	**0.000**	**11.043**
1998/99	6.908	0.000	56.208	3.942	**1.634**	7.785						**0.520**	**0.725**	**0.000**	**0.347**	**0.000**	**0.000**	**2.525**	**0.132**	**0.000**	**17.936**
1999/00					**0.985**							**1.617**	**2.608**	**0.000**	**5.414**	**0.790**	**0.705**	**3.427**	**5.255**	**0.000**	**15.617**
2000/01					**1.148**							**2.085**	**0.473**	**0.000**	**0.932**	**1.000**	**0.500**	**0.945**	**3.187**	**0.000**	**18.105**
2001/02					**1.307**	18.495					**0.577**	**3.381**	**3.932**	**0.000**	**7.252**	**1.577**	**1.406**	**5.018**	**2.062**	**0.003**	**18.436**
2002/03	**0.029**	**12.500**	**6.250**	**5.865**	**1.276**	35.334						**0.583**	**0.505**	**0.000**	**1.705**	**1.486**	**0.436**	**2.126**	**0.381**	**0.000**	**9.207**
2003/04		5.577	27.649		**1.364**	27.467			**5.632**		0.198	**0.535**	**1.181**	**0.000**	**2.848**	**1.171**	**0.802**	**6.314**	**1.364**	**0.000**	**15.700**
2004/05	**0.400**	7.058	12.173	5.274	**2.363**	21.329	**0.009**	**0.936**	**2.119**		**0.196**	**0.208**	**0.780**	**0.000**	**9.038**	**2.142**	**1.062**	**2.903**	**0.208**	**0.166**	**33.024**
2005/06	**1.234**	**0.250**	30.011	1.167	**1.590**	16.366	**0.003**	**3.688**	**2.440**		0.594	**0.291**	**2.559**	**0.000**	**3.360**	**1.194**	**0.336**	**3.182**	**3.149**	**0.379**	**22.766**
2006/07												**0.107**	**2.206**	**0.000**	**2.742**	**0.557**	**0.326**	**1.449**	**0.173**	**0.616**	**25.964**

Counts in ordinary font were made from aerial photographs; those in bold were ground counts.
Counts at Ichaboe, Lambert's Bay, Malgas, Jutten, Dasen and Dyer islands in 1956/57 assumed one bird to represent one pair (Rand 1963a, 1963b).
The count at Vondeling Island in 1956/57 was mainly of disused nests.
Counts of nests on photographs in 1956/57 of Cape Cross central and Bird Rock platforms and Mercury Island were from Cooper et al. (1982).
Counts at Seal, Penguin, North Reef, Pomona, Plumpudding, Sinclair, Schaapen and Meeuw islands in 1979/80 and at Jutten Island in 1989/90 were conducted outside the main breeding season.

reported by Rand (1963a; 1963b) and Cooper *et al*. (1982). Information for Lambert's Bay, Malgas, Jutten, Vondeling, Dassen and Dyer islands for 1985–1992 was from Crawford *et al*. (1992b) and Crawford and Dyer (1995).

Cape Cormorants arrive at the Namibian platforms in July. Increasing day length stimulates gonad development from August onwards and birds breed from October–February (Berry 1976). In South Africa's Western Cape, peak breeding usually takes place between September and February (Crawford *et al*. 1999b). Therefore, information was collated for split years commencing 1 July and ending 30 June. If more than one count was available for a locality in a split year, the highest count was taken as an estimate of the number breeding in that split year. It was attempted to conduct counts during the main breeding season of Cape Cormorants (September–February). Counts undertaken outside this period are indicated in Table 1. It is also indicated whether counts were made by ground or aerial surveys.

For ten localities, counts were available in most split years for the period since the late 1970s or mid 1980s. The missing counts were filled by linear interpolation between actual counts made at the locality. For these localities and periods, the counts and interpolated counts were smoothed using an algorithm described by Underhill *et al.* (2006). The weighted estimate is based almost entirely on the data from the target year and three years on either side of it. The same algorithm was applied to the combined counts at the six most important breeding localities for Cape Cormorants in the Western Cape for the period 1985/86–2006/07.

Information on the harvest of guano at the Namibian platforms was updated from Schwartzlose *et al*. (1999). The combined yield of the four platforms was smoothed using the same algorithm that was applied to relatively complete time series of counts, because in rare instances (12 of 190 possible cases) guano was not scraped in a season but allowed to accumulate until the next season. Banding has shown interchange of birds between the Cape Cross platforms and the Swakopmund and Bird Rock platforms (Rand 1963b; Berry 1976) and in 1974/75 birds abandoned breeding at the Swakopmund platform and moved to the platforms at Cape Cross (Crawford *et al*. 1980). Therefore, we considered the four guano platforms together. There were 11 split years for which counts of breeding Cape Cormorants were made at all four platforms. For these split years, the number of Cape Cormorants breeding at the platforms was regressed against the amount of guano collected at the platforms to investigate whether the guano yield could be used as a surrogate index of the number of Cape Cormorants breeding. Because the 11 complete counts extended over the 50-year period, with substantial gaps between most counts, no pre-whitening of residuals was undertaken prior to cross correlation.

Results

Guano platforms

Estimates of the number of Cape Cormorants breeding at selected localities in split years for which information is available are shown in Table 1. The overall number breeding at the four guano platforms increased from 12 000 pairs in 1956/57 to 74 000 pairs in 1978/79 (Figure 2). It averaged 56 000 pairs (s.d. = 12 000, n = 6) from 1988/89–1998/99 and 27 000 pairs (s.d. = 5 000, n = 3) from 2002/03–2005/06. The Swakopmund platform commenced operation in 1963 (Cooper *et al*. 1982). The first count of the number of Cape Cormorants at this platform was made in 1978/79, when about 44 000 pairs bred there. Subsequently, except in 2002/03, more birds bred at this than at any other platform (Table 1).

The number of Cape Cormorants breeding at the four platforms was significantly related to the production of guano at the platforms in the same split year ($r = 0.725$; $P < 0.02$; $n = 11$). When the outlying point for 1998/99 was excluded (Figure 3), the relationship improved ($r = 0.944$; $P < 0.001$; $n = 10$) and the number of Cape Cormorants (N, thousand pairs) was related to the guano production (G, thousand t) by the equation:

$$N = 24.165G - 11.867.$$

The smoothed production of guano at the platforms increased from 1 394 t in 1956/57 to 3 844 t in 1984/85 and then decreased to 1 562 t in 2005/06, suggesting a similar trend in the number of Cape Cormorants breeding at the platforms (Figure 2).

Southern Namibia

At the six main breeding localities off southern Namibia, there were about 3 000 pairs of Cape Cormorants in 1956/57 (Figure 2). In 1978/79, some 69 000 pairs were counted; in 1979/80 72 000 pairs. Counts suggest that the population off southern Namibia has fluctuated around 30 000 pairs since the mid 1980s. The highest counts recorded at Mercury, Ichaboe, Seal and Penguin islands and at North Reef were all made during the period 1978/79–1980/81. At Possession Island, the highest count was made in 1985/86 (Table 1).

Ichaboe Island was the most important breeding locality for Cape Cormorants off southern Namibia – counts exceeded 20 000 pairs on ten occasions, with a maximum of 46 000 pairs. The smoothed trend for Ichaboe Island showed a decrease after 1983/84 (Figure 2). At Seal Island, one count of 21 000 pairs was recorded but other counts were all less than 4 000 pairs (Table 1). At Penguin Island, counts of 18 000 pairs and 13 000 pairs were made in successive seasons and there were two counts of about 5 000 pairs. At no other locality were counts of 10 000 pairs or more recorded. At Mercury Island, two counts exceeded 5 000 pairs; at Possession Island there were four such counts. The highest count at North Reef was of 1 268 pairs in 1988/89. Estimates of the number of Cape Cormorants breeding at three small Namibian islands (Pomona, Plumpudding and Sinclair) to the south of Possession Island are available for eight seasons, for which the maximum combined count was about 600 pairs in 1995/96, 2001/02 and 2005/06.

Western Cape

At the six main localities for Cape Cormorants in the Western Cape, about 100 000 pairs bred in each of 1956/57, 1978/79 and 1988/89 (Figure 2). The number decreased to just 8 000 pairs in 1989/90 but increased to 90 000 pairs in 1991/92. It then decreased again to 25 000 pairs in 1994/95. From 1993/94–2005/06, it fluctuated about a mean level of 30 000 pairs (s.d. = 8 000; n = 14). Smoothed trends at individual colonies are shown in Figure 4. At Robben Island, no Cape Cormorants were recorded breeding between 1956/57 and 1984/85 (Kriel *et al*. 1980, RJMC pers. obs.). Sporadic breeding then occurred until 2001/02, after which the colony increased (Table 1).

At Dyer Island in 1985, for one group of breeding birds that was counted repeatedly the mean was 157 pairs (CV = 1.5%); for a second group it was 1 358 pairs (CV = 3.0%). It was estimated that the overall count of the number of Cape Cormorants breeding at the island (48 000 pairs) had a CV of 2.6%.

Overall

There are five split years in which counts of breeding pairs were made at each of the 16 most important localities for Cape Cormorants. In these split years, the combined counts were 111 000 pairs in 1956/57, 247 000 pairs in 1978/79, 157 000 pairs in 1992/93, 98 000 pairs in 2004/05 and 92 000 pairs in 2005/06. In 1985/86, counts were made at the 12 important islands in southern Namibia and the Western Cape, but not at the four platforms. If the relationship between number of birds breeding and guano production at the platforms is applied to the guano produced at the platforms in that season (3 945 t), there would have been 83 000 pairs at the platforms and 174 000 pairs at the 16 main localities. Similarly, in 1995/96 there would have been 42 000 pairs at the platforms (1 952 t) giving a total of 99 000 pairs for the 16 main localities. Therefore the breeding population of Cape Cormorants increased between 1956/57 and 1978/79 and then decreased (Figure 2). The increase resulted from more Cape Cormorants breeding at the platforms and in southern Namibia, while the number in the Western Cape was not much changed. The overall number in Namibia increased from 15 000 pairs in 1956/57 to 143 000 in 1978/79. There was a decrease in numbers off southern Namibia between 1978/79 and 1985/86, followed by decreases at the platforms and in the Western Cape in the early 1990s. In 2005/06, the number counted at the 16 main localities was 82% of that in 1956/57 and 37% of that in 1978/79.

Discussion

Reliability of estimates

Cooper *et al*. (1982) estimated the overall population of Cape Cormorants in 1977–1982 to be 277 000 pairs, based on the highest count obtained at any locality in this five-year period. In 1978/79, some 247 000 pairs bred at the 16 main localities, which represented 90% of the Cooper *et al*.'s estimation. Birds may abstain from breeding in years of unfavourable food supply (Crawford and Dyer 1995) and not all birds breeding in a given year may be present at the time of counting, so the numbers presented in this paper are minimum estimates of the overall population.

The Namibian platforms have held large numbers of Cape Cormorants. Previous assessments have attempted to estimate the number based on the surface area of the platforms and densities of birds (Rand 1963b; Berry 1976). As did Cooper *et al*. (1982), in this paper we use counts of nests to gauge the trend in numbers breeding at the platforms. A reasonable correspondence between nests counted and the guano yield at the platforms (Figure 3) suggests that trends in the number breeding at the platforms may be gauged from the guano records. Similarly, guano yield has been used as an index of the number of guano-producing seabirds in Peru (Crawford and Jahncke 1999).

At Ichaboe Island, the most important breeding locality in southern Namibia, and at the six most important breeding localities in the Western Cape, counts of nests were undertaken in many seasons since the late 1970s. Consequently, at these seven islands, the smoothed values probably provide a reasonable indication of trends in numbers of Cape Cormorants. These islands and the guano platforms supported 224 000 pairs in 1978/79, or 90% of the population in that season, so trends in the overall population are considered reliable for the latter half of the period investigated.

Almost all of Ichaboe Island was utilised by Cape Gannets in 1956/57–1967/68 (Rand 1963b). Therefore, the low estimate of the number of Cape Cormorants at that locality in 1956/57 is thought to be accurate. The numbers at other localities in southern Namibia were gauged from aerial photographs taken on 20 November 1956 (Rand 1963b). They may be underestimates, because in the 1990s and early 2000s many birds settled to breed at these localities after November, with peak counts often in January or February (JK unpublished records). It is also possible that the breeding season changed. In 1978/79, these localities supported

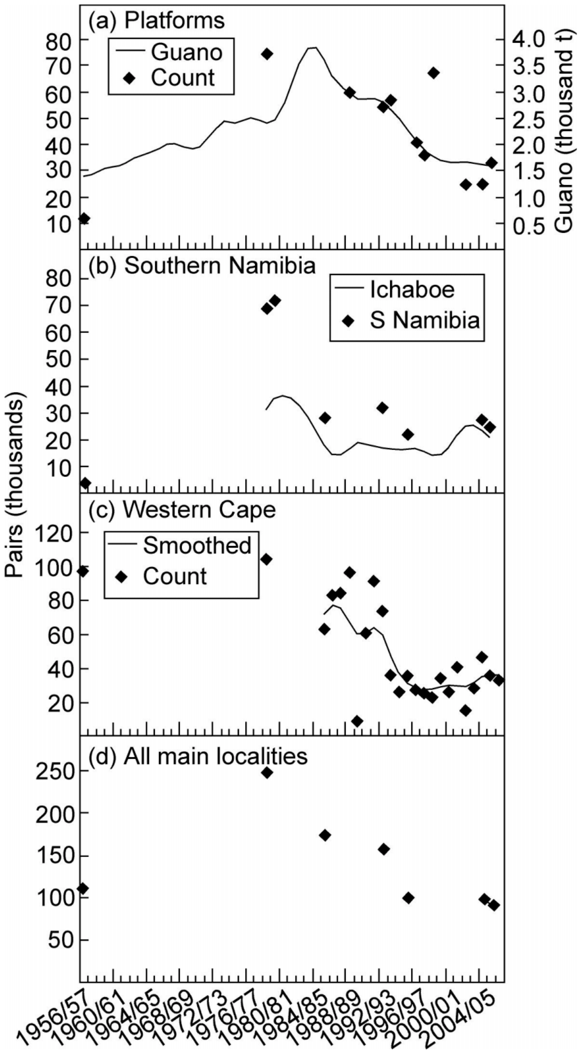

Figure 2: Numbers of Cape Cormorants breeding at (a) the Namibian platforms, (b) six islands off southern Namibia, (c) six islands in the Western Cape and (d) at these localities combined, 1956/57–2006/07. Smoothed trends are shown in (a) for the guano yield at the platforms, (b) the number of Cape Cormorants breeding at Ichaboe Island and (c) the number of Cape Cormorants breeding at six islands in the Western Cape

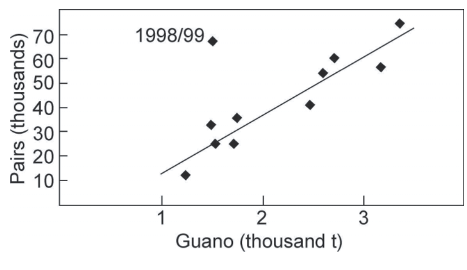

Figure 3: The relationship between the harvest of guano at the Namibian platforms and the number of Cape Cormorants breeding at these platforms, 1956/57–2006/07. The best-fitting regression line obtained after omiting the point for 1998/99 is shown

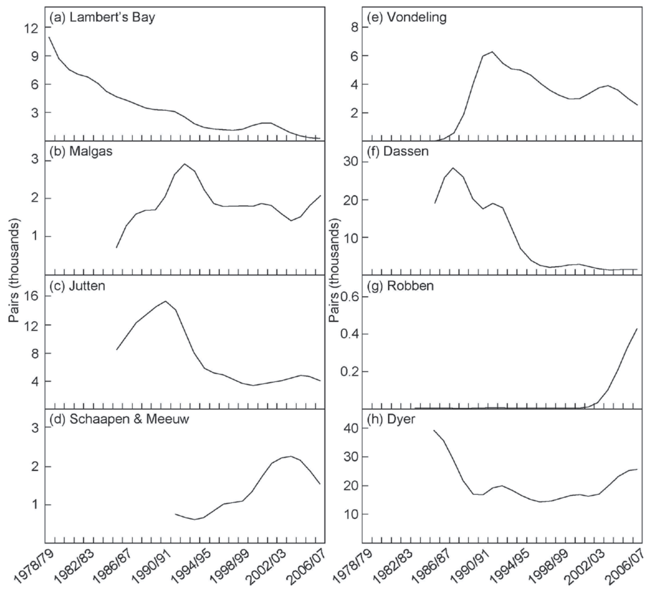

Figure 4: Smoothed trends in the number of Cape Cormorants breeding at (a) Lambert's Bay, (b) Malgas Island, (c) Jutten Island, (d) Schaapen and Meeuw islands, (e) Vondeling Island, (f) Dassen Island, (g) Robben Island and (h) Dyer Island, 1978/79–2006/07

47 000 pairs, compared to 3 000 estimated for 1956/57 (Table 1).

It is possible that numbers counted at some localities in the Western Cape in 1956/57 also underestimated the population. This was probably not the case for Lambert's Bay, Malgas and Jutten islands, where the counts made in 1956/57 were the highest, or close to the highest, recorded in the 50-year period (Table 1). At Dassen Island, the fact that Cape Cormorants bred only at the north of the island in both the 1956/57 and 1957/58 seasons (Rand 1963a), lends credence to the relatively low estimate for this island in 1956/57. At Vondeling Island, the counts for 1956/57 and 1978/79 were similar, but for Dyer Island the count in 1956/57 was some 32 000 pairs less than in 1978/79.

If, in 1956/57, the abundance in southern Namibia was underestimated by 44 000 pairs and that in the Western Cape by 32 000 pairs, the overall population would have been underestimated by 76 000 pairs. This is more than 50 000 pairs less than the estimated increase in the population of 133 000 pairs between the mid 1950s and the late 1970s, so it seems likely that there was a real increase in the population in this period.

Factors influencing trends in Cape Cormorants

The initial increase in the number of Cape Cormorants in Namibia can be attributed to two events that augmented the availability of breeding space, while still allowing an adequate supply of food. First, there was an increase in the number and size of guano platforms, with the Swakopmund platform only becoming operational in 1963 and some other platforms being extended after 1956/57 (Cooper *et al*. 1982). Additionally, as the Namibian sardine stock collapsed, its range contracted to the north, placing the remaining shoals increasingly distant from Namibia's Cape Gannet colonies. Most anchovy also were located well north of the gannet colonies (Crawford *et al*. 1987). However, these shoals were available to Cape Cormorants at the guano platforms, where in 1973/74 sardine and anchovy contributed 84% and 15% by mass of their diet, respectively (Berry 1976). Second, there was a decrease of Cape Gannets at Ichaboe Island, which increased the space available for breeding by Cape Cormorants (Crawford 1991). Here, and at Mercury Island, they were able to dive sufficiently deep to feed on pelagic gobies, which formed 84–100% by mass of their diet from 1978–1980 (Crawford *et al*. 1991) and 97% by number of their diet in 1982 (Duffy *et al*. 1987). By contrast, pelagic gobies were less available to the shallower-diving Cape Gannets and contributed only 10–28% by number of their diet at these localities during 1978–1982, a period of food scarcity for gannets. At this time pelagic gobies may have partially replaced sardine off Namibia (Crawford *et al*. 1985).

However, the food sources available to Cape Cormorants off Namibia later diminished (Boyer and Hampton 2001), and the number of birds breeding there decreased. Between the late 1970s and the mid 1980s, the number breeding in southern Namibia halved and did not subsequently recover (Figure 2). This followed a large decrease in the biomass of anchovy in Namibia, from nearly one million tones in 1973 to less than 0.2 million tones in 1984 and 1985 (Le Clus *et al*. 1987). By the conclusion of the 20th century, the size of the Namibian anchovy resource was no longer estimated because of its low abundance (G. Dalmeida, Ministry of Fisheries and Marine Resources, Namibia, pers. comm.). In 1984, a Benguela *Niño* caused mortality and southward displacement of some fish stocks in Namibia (Boyd *et al*. 1985; Le Clus 1985). The yield of guano at the platforms decreased in the early 1990s (Figure 2), suggesting that fewer Cape Cormorants bred there. In 1994, low levels of dissolved oxygen off Namibia caused extensive mortalities of fish and seals and greatly reduced the availability of anchovy, sardine and horse mackerel in Namibia (Hamukuaya *et al*. 1998; O'Toole and Bartholomae 1998). In 1994/95, Cape Cormorants only initiated breeding at Ichaboe Island in February (JK unpublished records). Then, in 1995, a Benguela *Niño* advected anomalously warm water as far south as Lüderitz, displacing fish stocks to the south and causing mortality off northern Namibia of sardine, horse mackerel and other fish (Gammelsrød *et al*. 1998). It thereby further reduced the availability of food to Cape Cormorants. At the Swakopmund platform, from 1994/95–1996/97 and in 2004/05 Cape Cormorants had poor breeding success (J. Klein, Salt Company, pers. comm.). Although a substantial number of Cape Cormorants bred at the platforms in 1998/99 (Figure 2), one of the owners of the guano platforms reported high mortality of cormorants at the end of the 20th century (W. Groenewald, Bird Rock Platform, pers. comm.).

From 1996 or earlier some Cape Cormorants bred at Ilha dos Tigres in southern Angola (Dean *et al*. 2002), probably moving north there on account of the shortage of food in Namibia. About 2 000 pairs bred at this island in 2001/02 (Simmons *et al*. 2006). On 25 November 2005, there were 2 630 pairs breeding at the island (BMD unpublished data).

In the Western Cape, a long-term decrease in Cape Cormorants at Lambert's Bay commenced in the late 1970s, whereas pronounced decreases at Malgas, Jutten, Vondeling and Dassen islands occurred in the early to mid 1990s (Figure 4). There was a large reduction in the overall number breeding in the Western Cape from the mid 1990s. Factors that influenced this decrease included mortality from avian cholera caused by the bacterium *Pasteurella multocida* (Crawford *et al*. 1992a; Williams and Ward 2002; Ward and Williams 2004; Waller and Underhill 2007), predation by Cape Fur Seals (*Arctocephalus pusillus*) (Marks *et al*. 1997; Ward and Williams 2004) and Great White Pelicans (Crawford *et al*. 1995) and a large eastward displacement of sardine off South Africa (Fairweather *et al*. 2006), decreasing its availability to seabirds breeding at islands west of Cape Point (Crawford *et al*. 2007). The increase in the number of Cape Cormorants breeding at Robben Island (Figure 4) resulted from the erection of a platform adjacent to the island in late 2003.

Cape Cormorants do not breed in large numbers to the east of Cape Agulhas (Cooper *et al*. 1982), where sardine have recently been plentiful (Fairweather *et al*. 2006) and where there has been a large increase in abundance of Cape Gannets (Crawford *et al*. 2007). In 1977–1981, 407 pairs of Cape Cormorants bred to the east of Cape Agulhas (Cooper *et al*. 1982). In 2003–2005, 253 pairs bred there (BMD unpublished information).

Clearly a variety of factors, which includes the abundance and distribution of food, the availability of suitable breeding habitat, disease and predation, has influenced trends in the population of Cape Cormorants. Available data suggest that the overall population is at more or less the same level as it was when the first survey was undertaken 50 years ago. In the intervening period, it expanded substantially before reverting to its initial level. Of particular concern for the future of the species has been a large reduction in the abundance of food off Namibia that has persisted for more than a decade (Boyer and Hampton 2001), a decreased availability of prey in the Western Cape, brought about more recently by an altered distribution of sardine (Fairweather *et al*. 2006), and an apparently increased frequency of outbreaks of avian cholera, which are generally associated with birds being under one or more forms of stress (Williams and Ward 2002).

Comparison with Cape Gannet

Similarly to the Cape Cormorant, the Cape Gannet feeds to a large extent on anchovy and sardine, the two fish species that have dominated the catch of purse-seine boats in the Benguela ecosystem (Hockey *et al*. 2005). However, the Cape Gannet does not breed at the guano platforms and it breeds at only three islands (Mercury, Ichaboe and Possession) off southern Namibia and two (Lambert's Bay and Malgas) in the Western Cape (Crawford *et al*. 2007). It additionally breeds at Bird Island in South Africa's Eastern Cape Province.

There have been similarities and differences in trends of Cape Cormorants and Cape Gannets. Numbers of Cape Cormorants breeding in southern Namibia may have increased between 1956/57 and 1978/79. The number of Cape Gannets in Namibia was stable from 1956/57–1967/69 and then decreased rapidly, as a result of a greatly reduced abundance of epipelagic fish prey that followed the collapse of the Namibian stock of sardine (Crawford *et al*. 2007). Unlike the Cape Gannet, the Cape Cormorant was initially able to feed substantially on pelagic gobies (Crawford *et al*. 1985). However, in the 1980s, numbers of both Cape Gannets and Cape Cormorants decreased off southern Namibia. Off South Africa's Western Cape, numbers of Cape Gannets remained relatively stable between the 1950s and the 1970s (Crawford *et al*. 2007), as did numbers of Cape Cormorants (Figure 2). The abundance of sardine in this region decreased in the 1960s, but that of anchovy probably increased (Crawford *et al*. 1987). In the Western Cape, numbers of Cape Gannets increased in the 1980s and early 1990s as South Africa's sardine stock recovered (Crawford *et al*. 2007), but the population of Cape Cormorants was stable (Figure 2), although a greatly reduced proportion of birds bred in 1989/90 and 1990/91 when there was a low abundance of anchovy (Crawford and Dyer 1995). Then Cape Cormorants decreased after 1992/93 (Figure 2) and Cape Gannets in the early 2000s (Crawford *et al*. 2007). As fish were displaced to the east (Fairweather *et al*. 2006), they probably remained available for a longer period to the Cape Gannet, which has a greater foraging range than the Cape Cormorant (Hockey *et al*. 2006).

In the Humboldt upwelling ecosystem off Peru and Chile, where anchovy and sardine also are the main forage species, Guanay Cormorants (*P. bougainvillii*) and Peruvian Boobies (*Sula variegata*) are considered to be the ecological equivalents of Cape Cormorants and Cape Gannets, respectively, in the Benguela ecosystem (Crawford *et al*. 2006). The Guanay Cormorant suffered a large decrease in abundance after the initiation of purse-seine fisheries, whereas there was long-term stability in the numbers of Peruvian Boobies, and the two species presently have equivalent population sizes (Crawford and Jahncke 1999). Once the most populous seabird in the Benguela ecosystem (Crawford *et al*. 1991), the Cape Cormorant is now less numerous than the Cape Gannet (Crawford *et al*. 2007). This seems largely attributable to its smaller foraging range and less flexible foraging strategy. The Cape Gannet, for example, is able to feed on fishery discards as well as catch its own prey (Hockey *et al*. 2005). The ability of Cape Cormorants to colonise artificial habitat, such as platforms, provides opportunity to manage any long-term mismatch between the distribution of the prey of Cape Cormorants and its breeding localities.

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