Cape cormorants decrease, move east and adapt foraging strategies following eastward displacement of their main prey


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Cape cormorants decrease, move east and adapt foraging strategies following eastward displacement of their main prey

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Introduction

Cape cormorants Phalacrocorax capensis are endemic to southern Africa, where their usual non-breeding range extends from Lobito, Angola (12° S), on the west coast to Maputo Bay (formerly Delagoa Bay), Mozambique (25° S), on the east coast (Cooper et al. 1982). They breed from southern Angola to South Africa’s Eastern Cape province (Cooper et al. 1982; Dean et al. 2002), almost exclusively within the area of jurisdiction of the Benguela Current Commission (BCC), which extends from 5° S off Angola to 27° E off South Africa. The only known record of breeding outside this area is of at least one nest at Hole-in-the-Wall, Eastern Cape, in 1925 or 1926 (Cooper et al. 1982).

In 1977–1981, the global population was estimated to be approximately 107 000 pairs in 1977–1981 to 57 000 pairs in 2010–2014. Although four colonies had >10 000 pairs in 1977–1981, there was just one such colony in 2010–2014. Almost all the decrease occurred after the early 1990s off north-west South Africa, between the Orange River estuary and Dassen Island. South of this, the number breeding in the two periods was stable, with some colonies being formed or growing rapidly in the 2000s. The proportion of South Africa’s Cape cormorants that bred south of Dassen Island increased from 35% in 1977–1981 to 66% in 2010–2014, with the opposite situation observed in the north-west. This matched a shift to the south and east in the distributions of two of the Cape cormorant’s main prey species, anchovy Engraulis encrasicolus and sardine Sardinops sagax.

In 2014, an apparent scarcity of prey in the north-west resulted in Cape cormorants attempting to take bait from hooks of fishing lines over an extended period, a behaviour not previously recorded. The number of Cape cormorants breeding in the south may be constrained by the absence of large islands between Dyer Island in the west and Algoa Bay in the east. If so, it may be possible to bolster the southern population through the provision of appropriate breeding habitat, such as platforms, or restricting human disturbance at suitable mainland cliff breeding sites.

Keywords: colony size, distribution change, food availability, foraging behaviour, Phalacrocorax capensis, population decrease
et al. 2007; Kemper and Simmons 2015), the latter a decline from 171,000 in 1977–1981. In 2015, the Cape cormorant was listed as Endangered in Namibia, in South Africa and globally (BirdLife International 2015; Cook 2015; Kemper and Simmons 2015). Cape cormorants had the most severe decrease in atlas-reporting rates of any bird species in South Africa between 1987–1991 and 2007–2014 (Underhill and Brooks 2014).

Here we update information on the numbers of Cape cormorants breeding in South Africa and provide details of decreases at colonies in the north-west and growth of colonies in the south. We consider how the decrease in overall numbers influenced colony size and present observations on unusual recent foraging strategies of Cape cormorants, which support the hypothesis that food scarcity is driving population shifts in this species.

Material and methods

An estimate was made of the number of Cape cormorants breeding in South Africa in 2010–2014, following the methods used for 1977–1981 and 2009–2013 (Cooper et al. 1982; Crawford et al. 2015). Active nest sites (defined as sites defended by a pair of birds, showing evidence of recent nest construction or nests with eggs, chicks or adults) were counted at all major and most known breeding localities. When unattended chicks were found in crèches away from nests, their number was divided by three (the approximate mean clutch size; Berry 1976) to estimate the number of nests they represented, because nests at which these chicks were reared would not have been counted. Remainders were taken to represent further sites; e.g. four, five or six chicks would be taken to represent two sites (Cooper et al. 1982; Crawford et al. 2015). This does not account for egg and chick mortality. However, replacement laying may occur (Hockey et al. 2005) and the contribution of nests assumed from counts of chicks in crèches to the overall numbers breeding was small (Crawford et al. 2015).

The largest numbers of active nest sites recorded at each breeding locality during 2010–2014 were summed because not all localities were visited each year. Cape cormorants have an extended breeding period, often...
breed asynchronously (so that visits to localities may not coincide with peak breeding), sometimes skip breeding and often show strong fidelity to breeding localities (Berry 1976; Cooper et al. 1982; Crawford et al. 1992a, 1999a). However, some birds may move to nearby localities, which could lead to an overestimation of the population if the same birds were counted at more than one locality in a given period (Randall et al. 1981; Crawford et al. 1994). Numbers at small colonies were counted accurately, and the coefficient of variation of counts repeated on the same day at a large colony of 48 000 pairs at Dyer Island was 2.6% (Crawford et al. 2007).

Annual estimates of numbers breeding were available for 10 localities or groups of localities for 1988–2014 (or a portion of this period): Lambert’s Bay, Malgas Island and Jutten Island, Meeuw Island and Schaapen Island, Vondeling Island, Dassen Island, Robben Island, Stony Point, Dyer Island, Knysna Heads to Tsitsikamma No. 12 stacks, as well as islands in Algoa Bay (Figure 1). Localities were grouped when they were close together and in similar habitats. For two periods (1977–1981 and 2010–2014), for which more or less complete census information was available for Cape cormorants in South Africa, the mean number of pairs breeding at localities was calculated and the numbers of localities having 1–10, 11–100, 101–1 000, 1 001–10 000 and >10 000 pairs were plotted. Colony sizes were tested for a normal distribution using the Kolmogorov–Smirnov test. They were found not to be normally distributed, but to be consistent with a lognormal distribution and were transformed accordingly. The resultant geometric means and multiplicative standard deviations were used in a two-tail Student’s t-test to investigate whether colony sizes differed significantly between 1977–1981 and 2010–2014. The Chi-squared test was used to examine whether numbers in the five colony-size-intervals indicated above (1–10, etc.) differed between the two periods.

In 2014, reports were received that Cape cormorants were taking bait from handlines used to fish for snoek Thyrsites atun between St Helena Bay and Dassen Island on the West Coast. Cape cormorants had not previously been known to take bait from fishing lines (Hockey et al. 2005). Therefore, further information was sought from observers in the area. On the South Coast, in 2014 and 2015 unusually large numbers of Cape cormorants visited two lakes between Wilderness and Knysna to feed. Notes were made of these events. In 2014, roosts were formed between feeding bouts, usually on the water, but occasionally on the partially flooded shoreline of one of the lakes (Rondevlei) where searches were conducted for regurgitations. Those found were collected and later examined for fish otoliths, which were identified to species level, using the atlas of Smale et al. (1995).

Results

Population trends

There are 53 localities in South Africa at which Cape cormorants have been recorded breeding (Table 1). At these, the maximum number of pairs ranged from one each at Robbe Island and Owen Island in the Northern Cape to almost 50 000 at Dyer Island, with a mean maximum of approximately 4 000 pairs. Until 2014, five localities (Lambert’s Bay, Jutten Island, Vondeling Island, Dassen Island and Dyer Island) had at some time supported >10 000 pairs and six others (Orange River estuary, Malgas, Meeuw, Schaapen and Robben islands and Stony Point) >1 000 pairs. These localities are all west of Cape Agulhas (Figure 1).

In 1977–1981, 38 of the localities were visited, breeding was noted at 30 and the sum of the maximum counts at the occupied localities was 106 824 pairs (Table 1, Cooper et al. 1982). This value is unlikely to underestimate substantially the actual population because, of the 15 colonies not surveyed in 1977–1981, the sum of the maximum counts at any time was 3 820 pairs. In 2010–2014, breeding occurred at 37 of 48 localities that were surveyed. At these, the maximum counts for this period totalled 56 987 pairs (Table 1), which is 53% of the value for 1977–1981. The sum of maximum counts at any time of the five localities not visited in 2010–2014 was 634 pairs, so again their omission would not have had a major impact. When counts at the 35 localities that were surveyed in both 1977–1981 and 2010–2014 were compared, summed maxima decreased by 48% between these periods.

Off north-west South Africa (Northern Cape and Western Cape [north], i.e. Bokpunt northwards), there were large decreases in numbers of Cape cormorants breeding at Lambert’s Bay, Malgas Island, Jutten Island and Dassen Island between 1988 and 2014 (Figure 2). The decreases all occurred between 1988 and the mid-1990s. There was limited recovery at Lambert’s Bay in the late 1990s and early 2000s, followed by another decrease, whereas at Malgas Island, Jutten Island and Dassen Island breeding remained depressed after the mid-1990s. Numbers of Cape cormorants breeding at Meewu Island and Schaapen Island in Langebaan Lagoon increased in the late 1990s and early 2000s, before decreasing in fluctuating manner after the mid-2000s (Figure 2). Numbers at Vondeling Island peaked in 1994.

At South Africa’s northernmost breeding locality, the Orange River estuary, nearly 8 000 pairs bred in 1976 (Frost and Johnson 1977), but no breeding has been reported there since 1993 (Anderson et al. 2003; Department of Environmental Affairs [DEA] unpublished data). Whereas the mean number of Cape cormorants (individuals) counted at the Orange River estuary was 6 400 (SD = 3 861; n = 5) from 1980 to January 1994, it was 212 (SD = 612; n = 16) from April 1994 to 2001 (Anderson et al. 2003). Therefore, the decrease in Cape cormorants off north-west South Africa after the early 1990s extended as far north as the Namibian border.

In the south (Western Cape [south-west and east], Eastern Cape), there were large increases in numbers of Cape cormorants breeding at Robben Island after 2004 and at Stony Point after 2011 (Figure 2). Brooke (1983) inferred breeding by Cape cormorants at two colonies at Robben Island in 1652. There are no further records until six nests were observed on the breakwaters in 1991 and four nests in 1992 (Kriel et al. 1980; Cooper et al. 1992; DEA unpublished data). Three nests were seen at Robben Island in 2001 and >100 in 2004; no breeding was observed between 1993 and 2000 or in 2002 and...
Table 1: The maximum counts of Cape cormorant breeding pairs at known South African colonies in 1977–1981 (from Cooper et al. 1982, * corrected), in 2010–2014 and in all years. The year(s) of the maximum counts are indicated

<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Maximum count</th>
<th>Year(s) of maximum count</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Northern Cape</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orange River estuary</td>
<td>28°38′ S</td>
<td>16°26′ E</td>
<td>250</td>
<td>0</td>
</tr>
<tr>
<td>Boegoeberg (stack south of Humewood)</td>
<td>28°46′ S</td>
<td>16°34′ E</td>
<td>88</td>
<td>88</td>
</tr>
<tr>
<td>Robbie Island</td>
<td>29°15′ S</td>
<td>16°52′ E</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Owen Island</td>
<td>29°16′ S</td>
<td>16°52′ E</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Matthew Island</td>
<td>29°17′ S</td>
<td>16°52′ E</td>
<td>405</td>
<td>629</td>
</tr>
<tr>
<td>Robeiland, Kleinzee</td>
<td>29°34′ S</td>
<td>17°00′ E</td>
<td>182</td>
<td>30</td>
</tr>
<tr>
<td>Penguin Rock</td>
<td>29°36′ S</td>
<td>17°00′ E</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td><strong>Western Cape (north)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stack south of Cliff Point</td>
<td>31°36′ S</td>
<td>18°07′ E</td>
<td>124</td>
<td>30</td>
</tr>
<tr>
<td>Elephant Rock</td>
<td>31°39′ S</td>
<td>18°09′ E</td>
<td>67</td>
<td>27</td>
</tr>
<tr>
<td>Cliff south of Strandfontein</td>
<td>31°48′ S</td>
<td>18°14′ E</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Bird Island, Lambert’s Bay</td>
<td>32°05′ S</td>
<td>18°18′ E</td>
<td>13 519</td>
<td>115</td>
</tr>
<tr>
<td>Berg River mouth</td>
<td>32°46′ S</td>
<td>17°00′ E</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Stompnes Bay rocks</td>
<td>32°48′ S</td>
<td>17°53′ E</td>
<td>25</td>
<td>8</td>
</tr>
<tr>
<td>Klein Paternoster rocks</td>
<td>32°48′ S</td>
<td>17°53′ E</td>
<td>81</td>
<td>81</td>
</tr>
<tr>
<td>Cape Columbine rocks</td>
<td>32°49′ S</td>
<td>17°51′ E</td>
<td>18</td>
<td>169</td>
</tr>
<tr>
<td>Malgas Island</td>
<td>33°03′ S</td>
<td>17°55′ E</td>
<td>8 708</td>
<td>1 914</td>
</tr>
<tr>
<td>Marcus Island</td>
<td>33°03′ S</td>
<td>17°58′ E</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Jutten Island</td>
<td>33°05′ S</td>
<td>18°00′ E</td>
<td>1981</td>
<td>124</td>
</tr>
<tr>
<td>Meeuw Island</td>
<td>33°06′ S</td>
<td>17°54′ E</td>
<td>25</td>
<td>28</td>
</tr>
<tr>
<td>St Croix Island</td>
<td>33°06′ S</td>
<td>17°53′ E</td>
<td>6</td>
<td>421</td>
</tr>
<tr>
<td>Steenbras Bay rock</td>
<td>33°06′ S</td>
<td>17°54′ E</td>
<td>182</td>
<td>30</td>
</tr>
<tr>
<td>Robben Island</td>
<td>33°09′ S</td>
<td>17°59′ E</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td><strong>Western Cape (south-west)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Koeberg NPS</td>
<td>33°40′ S</td>
<td>18°26′ E</td>
<td>0</td>
<td>300</td>
</tr>
<tr>
<td>Robben Island</td>
<td>33°48′ S</td>
<td>18°22′ E</td>
<td>0</td>
<td>2 166</td>
</tr>
<tr>
<td>Cape Town waterfront</td>
<td>33°54′ S</td>
<td>18°27′ E</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Duikerklip</td>
<td>33°47′ S</td>
<td>18°28′ E</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Flora Bay, Die Josie</td>
<td>33°47′ S</td>
<td>18°30′ E</td>
<td>643</td>
<td>400</td>
</tr>
<tr>
<td>Cape Point</td>
<td>33°49′ S</td>
<td>18°31′ E</td>
<td>9</td>
<td>500</td>
</tr>
<tr>
<td>Batsata Cove</td>
<td>33°50′ S</td>
<td>18°32′ E</td>
<td>150</td>
<td>570</td>
</tr>
<tr>
<td>Smitswinkel Bay cliffs</td>
<td>33°51′ S</td>
<td>18°33′ E</td>
<td>0</td>
<td>671</td>
</tr>
<tr>
<td>Simon’s Town</td>
<td>33°52′ S</td>
<td>18°34′ E</td>
<td>0</td>
<td>54</td>
</tr>
<tr>
<td>Strandfontein sewage works</td>
<td>33°53′ S</td>
<td>18°35′ E</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Seal Island, False Bay</td>
<td>33°54′ S</td>
<td>18°36′ E</td>
<td>0</td>
<td>54</td>
</tr>
<tr>
<td>Stony Point</td>
<td>33°55′ S</td>
<td>18°37′ E</td>
<td>0</td>
<td>1 279</td>
</tr>
<tr>
<td>Prekstoel, Kleinmond</td>
<td>33°56′ S</td>
<td>19°02′ E</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>Dyer Island</td>
<td>33°57′ S</td>
<td>19°03′ E</td>
<td>35 580</td>
<td>30 524</td>
</tr>
<tr>
<td>Geyser Island</td>
<td>33°58′ S</td>
<td>19°04′ E</td>
<td>545</td>
<td>0</td>
</tr>
<tr>
<td>Die Dam</td>
<td>33°59′ S</td>
<td>19°05′ E</td>
<td>c. 50</td>
<td>50</td>
</tr>
<tr>
<td><strong>Western Cape (east)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>De Mond</td>
<td>34°02′ S</td>
<td>20°07′ E</td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td>Waenhuiskranz</td>
<td>34°03′ S</td>
<td>20°14′ E</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>De Hoop, Vaalkrans</td>
<td>34°04′ S</td>
<td>20°34′ E</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Gericks’ Point</td>
<td>34°05′ S</td>
<td>22°45′ E</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Knynea Heads</td>
<td>34°06′ S</td>
<td>23°03′ E</td>
<td>435</td>
<td>435</td>
</tr>
<tr>
<td>Robberg</td>
<td>34°07′ S</td>
<td>23°21′ E</td>
<td>734</td>
<td>734</td>
</tr>
<tr>
<td>Tsitsikamma No. 12 stacks</td>
<td>34°08′ S</td>
<td>23°35′ E</td>
<td>75</td>
<td>834</td>
</tr>
<tr>
<td><strong>Eastern Cape</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jahleel Island</td>
<td>33°45′ S</td>
<td>25°42′ E</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Brenton Island</td>
<td>33°46′ S</td>
<td>25°46′ E</td>
<td>88</td>
<td>68</td>
</tr>
<tr>
<td>St Croix Island</td>
<td>33°47′ S</td>
<td>25°46′ E</td>
<td>88</td>
<td>68</td>
</tr>
<tr>
<td>Seal Island, Algoa Bay</td>
<td>33°50′ S</td>
<td>26°17′ E</td>
<td>44</td>
<td>116</td>
</tr>
<tr>
<td>Stag Island</td>
<td>33°50′ S</td>
<td>26°17′ E</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Hole-in-the-Wall</td>
<td>33°50′ S</td>
<td>26°17′ E</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td>106 824</td>
<td>56 987</td>
</tr>
</tbody>
</table>

b Published records were consulted, as well as unpublished data of Branch: Oceans & Coasts, Department of Environmental Affairs and Percy FitzPatrick Institute of African Ornithology, University of Cape Town. The following records of breeding reported in Du Toit et al. (2002) were not accepted because it was confirmed from inspection of original records that they were of roosting and not breeding Cape cormorants: c. 200 pairs at Seal Island, False Bay, on 22 October 2001; 111 pairs at Stony Point on 20 June 2001; and <20 pairs at Bird Island, Algoa Bay, on 12 August 1997.
Figure 2: Trends in numbers of Cape cormorants at frequently monitored South African colonies or groups of colonies, 1988–2014. Values are shown as the proportion of the maximum number recorded breeding at each locality or group of localities during 1988–2014. Gaps in the datasets reflect a lack of information for the relevant years.
2003 (DEA unpublished data). Breeding was first detected at Stony Point in 2010 (51 nests, JH unpublished data, DEA unpublished data). At Dyer Island, between 1988 and 2014 there was no noticeable trend, but large fluctuations, in numbers breeding (mean = 19 643 pairs; SD = 7 955). Dyer Island supported the largest number of Cape cormorants in South Africa in both survey periods, representing 33% of the population in 1977–1981 and 54% in 2010–2014 (Table 1). Farther east, there was a marked increase of Cape cormorants breeding on coastal cliffs or stacks between Knysna and Tsitsikamma, which appears to have started after 2003 (Whittington 2004; Figure 2).

Cape cormorants nested in unknown numbers at Knysna Heads (Coney Glen) in 1973 and 1974 (Cooper et al. 1982), whereas 435 pairs bred there in 2012. At Robberg, approximately 200 Cape cormorants were roosting in the summers of 2011 and 2012; this increased to 500 in 2013 and 5 000 in April 2014 (CapeNature unpublished data). On aerial photographs of the peninsula taken in December 2014, 734 nests were counted. At Tsitsikamma, 75 pairs bred in 1980 (Crawford 1983), there were 37 nests and 268 fledged young in 2003 (Whittington 2004) and 834 pairs bred in 2010 (RMR unpublished data). Numbers breeding at islands in Algoa Bay increased after 2004 (Figure 2).

Off north-west South Africa, numbers of Cape cormorants decreased from 70 000 pairs in 1977–1981 to 19 000 pairs in 2010–2014, whereas in the south approximately 37 000 pairs bred in both periods (Figure 3). This resulted in the proportion breeding in the north-west decreasing from 65% to 34% and the proportion breeding in the south increasing from 35% to 66%.

The mean number of Cape cormorants breeding per locality in South Africa was 3 561 pairs (SD = 8 276; range 1–35 524; n = 30 colonies) in 1977–1981, which decreased by 56% to 1 540 pairs (SD = 5 126; range 1–30 524; n = 37) in 2010–2014. After logarithmic transformation of colony sizes, means were not significantly different between the two periods (t = 0.113, df = 65, p = 0.91). In 1977–1981, four localities had >10 000 pairs, but there was only one colony of equivalent size in 2010–2014 (Figure 4). However, the Chi-squared test showed no significant difference between periods in numbers of colonies within the size categories that are indicated in Figure 4 (χ² = 6.57, p = 0.16). This was also the case when the test was conducted for colonies in north-west (χ² = 7.20, p = 0.13) and south (χ² = 2.66, p = 0.61) South Africa. Localities having >10 000 pairs and >1 000 pairs supported 82% and 97%, respectively, of the South African population in 1977–1981, compared to 54% and 92% of the population in 2010–2014.

**Novel foraging behaviours**

W Croome (South African Commercial Linefish Association, pers. comm.), a snoek fisher, indicated that during May and June 2014 Cape cormorants (the species was confirmed from photographs) attempted to take bait from handlines used to fish for snoek from skiboats of approximately 7 m length and crewed by 8–10 men. This occurred in St Helena Bay and near Dassen Island at water depths of approximately 36 m and at distances up to 12 km and 6 km from the coast, respectively. Most fishing took place after 10:00. The cormorants foraged in flocks of up to 100 birds. The behaviour lasted approximately 25 days and affected most (30–40) skiboats fishing for snoek in the region on those days. The bait in use at the time was saury Cololabis saira or Scomberesox saurus, which took 2–3 seconds to sink below the sea surface. Cape cormorants did not attempt to hunt live prey, but concentrated on taking bait shortly after casting while it was still at the surface, or occasionally to depths of approximately 10 m. However, bait was not taken from lines that were being hauled in. Some Cape cormorants successfully took bait without being hooked, but others were hooked on the bill or throat and some swallowed both bait and hook (as evidenced by a photograph). T van Boom (Lucky Star [Oceana Group Ltd], pers. comm.) reported that a few Cape cormorants were hooked in the neck or body as a result of fishers striking when they felt nibbles at the bait. W Croome
(pers. comm.) noted that hooked birds were released once the hook had been removed or the line cut, but their subsequent fate was unknown. However, some mortality occurred when cormorants drowned or were badly injured and were subsequently euthanised by fishers. He observed that snoek fishers were frustrated by the loss of bait and employed various strategies to avoid such loss. These included pulling up lines and moving elsewhere, and ‘flying’ plastic bags from fishing rods to keep birds away from lines, a similar principle to the tori lines used to keep pelagic seabirds away from longlines or trawl gear (e.g. Petersen et al. 2009). Both tactics had some success, but shooting into the air to drive birds away proved ineffective because the cormorants dived into the water and then returned to the baited hooks. He stated that fishers did not attempt to kill cormorants. Neither W Croome nor T van Boom had previously observed or heard about Cape cormorants taking bait from handlines. M Potgieter (Lucky Star, pers. comm.) advised that during the period in which Cape cormorants were eating bait, most anchovy and sardine were deep in the water column and most catches of these fish species by Lucky Star were made where nets could reach the sea bed, with few from surface shoals.

In the winters of 2014 and 2015, Cape cormorants visited the coastal lakes of Eilandvlei and Rondevlei of the Touw River system between Wilderness and Knysna to feed. In the previous 25 years, they had not been observed at Rondevlei and only in much smaller numbers at Eilandvlei (RMR pers. obs.). In 2015, they were first seen at Eilandvlei on 30 June, approximately 1 400 were present there on 28 July, and they moved to Rondevlei in mid-August. A similar pattern was observed in 2014, when they were present at the lakes during the day, but moved away at night to roost, mostly on sea cliffs west of Gericke’s Point (RMR pers. obs.; Figure 1). Observations at the cliffs showed that feeding groups of cormorants returning to the roosts came both from the sea and the lakes. These observations were supported by analyses of 20 regurgitations recovered at Rondevlei in 2014, which revealed the occurrence of three fish species: anchovy, a marine species (n = 2); Cape halibek Hyporhampus capensis, an estuarine and marine species (n = 1); and Cape silverside Atherina breviceps, an estuarine or inshore marine species (n = 2) (Heemstra and Heemstra 2004).

**Discussion**

**Altered distribution**

A decreased relative importance for Cape cormorants in South Africa of localities in the north-west and an increased contribution of those in the south has been noted previously and accords with a similar shift to the south and east in the breeding distributions of several other seabirds (Crawford et al. 2008, 2014, 2015) and those of their prey species (Roy et al. 2007; Cockcroft et al. 2008; Coetzee et al. 2008; Blamey et al. 2015). For Cape cormorants, the shift is attributable both to a decrease in numbers breeding at northern localities, especially at the formerly important marine localities of Lambert’s Bay and Malgas Island, Jutten Island, Vondeling Island and Dassen Island, and to growth of some colonies and formation of new colonies in the south (Figure 2).

The decrease of Cape cormorants in western South Africa after the early 1990s was influenced by considerable mortality from avian cholera Pasteurella multocida (Crawford et al. 1992b; Williams and Ward 2002; Waller and Underhill 2007) and by substantial predation of eggs, chicks or grown birds by kelp gulls Larus dominicanus, great white pelicans Pelecanus onocrotalus and Cape fur seals Arctocephalus pusillus pusillus (Marks et al. 1997; Ward and Williams 2004; Machado 2010; Mwema et al. 2010; Voorbergen et al. 2012; Makhado et al. 2013). However, whereas several northern colonies decreased, the one at Dyer Island, where some of these factors also operated, remained stable (Figure 2). This suggests that at Dyer Island breeding success or immigration from other colonies was sufficient to offset heavy mortality, whereas this was not the case at localities between Lambert’s Bay and Dassen Island.

The establishment of new colonies at Robben Island in 2004, at Stony Point in 2010 and at Robberg in 2014 must have resulted from immigration. Immigration also may have assisted growth at other southern colonies, e.g. at Knysna Heads and Titsikamma. The eventual success of Cape cormorants in forming a colony at Robben Island followed the deployment of a small platform adjacent to the island in late 2003, which was occupied by the cormorants in 2004 (Crawford et al. 2007). The primary reason for the platform was to provide alternative breeding space for bank cormorants Phalacrocorax neglectus when breakwaters at Robben Island’s harbour were being extended and repaired, although bank cormorants did not use the platform. When the platform was removed, Cape cormorants moved onto the harbour’s refurbished breakwaters to breed alongside bank cormorants (DEA unpublished data). At Stony Point, African penguins Spheniscus demersus, bank, crowned Microcarbo coronatus and white-breasted cormorants Phalacrocorax lucidus were already breeding prior to the initiation of breeding by Cape cormorants (Crawford et al. 1999b, 2011, 2012, 2013) and may have attracted Cape cormorants to the locality. At Robberg Nature Reserve, the breeding ledges used by Cape cormorants are adjacent to the colony of Cape fur seals and so are relatively shielded from mainland predators and disturbance by humans.

A reduced relative importance for Cape cormorants has also been noted in South Africa after the early 1990s was influenced by considerable mortality from avian cholera Pasteurella multocida (Crawford et al. 1992b; Williams and Ward 2002; Waller and Underhill 2007) and by substantial predation of eggs, chicks or grown birds by kelp gulls Larus dominicanus, great white pelicans Pelecanus onocrotalus and Cape fur seals Arctocephalus pusillus pusillus (Marks et al. 1997; Ward and Williams 2004; Machado 2010; Mwema et al. 2010; Voorbergen et al. 2012; Makhado et al. 2013). However, whereas several northern colonies decreased, the one at Dyer Island, where some of these factors also operated, remained stable (Figure 2). This suggests that at Dyer Island breeding success or immigration from other colonies was sufficient to offset heavy mortality, whereas this was not the case at localities between Lambert’s Bay and Dassen Island.

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(Crawford et al. 2014), as well as by a net deficit in energy during foraging for most Cape gannets tracked from Malgas Island between 2011 and 2014 (Grémillet et al. 2016).

The decrease of Cape cormorants off north-west South Africa between 1977–1981 and 2010–2014 (c. 50 000 pairs) was approximately equivalent to the summed decreases at the five main breeding localities in the region, suggesting that food availability became insufficient to support large colonies, whereas some smaller colonies were able to maintain their sizes (Table 1). In the Humboldt ecosystem off western South America, numbers of guanay cormorants P. bougainvillii, which feed in large flocks (Johnsgard 1993), decreased in Peru by an order of magnitude soon after the introduction of a purse-seine fishery for anchoveta Engraulis ringens (Crawford and Jahnncke 1999). In November 2008, Cape cormorants brooding small chicks expended significantly greater foraging effort at Malgas Island and Dassen Island in the north-west than at Dyer Island in the south (Hamann et al. 2012). The atypical behaviour of Cape cormorants between St Helena Bay and Dassen Island in attempting to take bait from handlines over a period of several weeks in 2014 suggests insufficient availability of their usual prey at the time. If prey is too deep for them to catch, as may have been the case in this instance, it will be unavailable. Mean dive depth of Cape cormorants is c. 10 m (maximum 37 m, Ryan et al. 2010; Cook et al. 2012).

Within this context, Dyer Island represents one of the most important colonies for the species in South Africa, not only in terms of numbers of breeding pairs (Table 1), but also by reason of its location on the South Coast, closer to the core of the new distribution of anchovy and sardine (Roy et al. 2007; Coetzee et al. 2008). However, despite this more advantageous position, birds from Dyer Island also suffer from food shortage. In November 2011, estimated anchovy biomass in South Africa decreased to a level it had not reached since 1993–1998 (Shabangu et al. 2011). Although 24 000 pairs of Cape cormorants were breeding on Dyer island in early November 2011, only c. 500 pairs were still actively breeding by the end of the month, the rest having abandoned their nests (most of which contained chicks [TRC pers. obs.]). Scarcity of food near Dyer Island was further illustrated by the maximum foraging range in mid-November of breeding birds equipped with GPS loggers. Cape cormorants foraged as far as False Bay, 80 km from the colony, a distance never reached by birds during the four other years when GPS loggers were deployed on birds at Dyer Island (TRC unpublished data).

Interestingly, in 2011, a new colony of c. 300 pairs settled 65 km east of Dyer Island, on the shore near the mouth of the Heuningnes River (34°42′ S, 20°07′ E) in De Mond Nature Reserve (N Hess, formerly CapeNature, pers. comm.). Breeding on a continental beach is a behaviour that is unusual in this species, because it exposes not only eggs and chicks but also adults to land predators like black-backed jackals Canis mesomelas, Cape clawless otters Aonyx capensis and mongooses.

Nesting in a suboptimal environment accords with birds trying to adjust the position of their breeding locality to the recent eastward displacement of anchovy and sardine in a seascape where the only island between Dyer Island and the islands of Algoa Bay, 600 km to the east, is the small Seal Island at Mossel Bay, which is fully occupied by Cape fur seals. Similar eastward shifts have been recorded for other seabirds in the Benguela ecosystem that feed mainly on anchovy and sardine (Crawford et al. 2015). However, Cape cormorants have not been as successful in adjusting their breeding distribution as, for example, Cape gannets, for which >70% of South Africa’s population now breeds in the Eastern Cape (Crawford et al. 2014). It is unclear why larger numbers have not yet settled at islands in Algoa Bay, because Cape cormorants are regular visitors in varying numbers farther east to KwaZulu-Natal between June and November, when they feed on the winter ‘sardine run’ (Cyrus and Robson 1980; Taylor et al. 1999). Possibly large numbers of African penguins and Cape gannets at the islands (Crawford et al. 2009) compete for breeding space or reduce concentrations of prey in their vicinity (e.g. Gaston et al. 2007).

**Conservation status**

In 1977–1981, 16 localities (10 in Namibia and six in South Africa) supported >99% of the total population of Cape cormorants (Cooper et al. 1982). The six South African localities (Lambert’s Bay, Malgas Island, Jutten Island, Vondeling Island, Dassen Island and Dyer Island) were all in the Western Cape and together held c. 100 000 pairs in the 1956/1957, 1978/1979 and 1988/1989 breeding seasons and c. 90 000 pairs in 1991/1992, but their combined total subsequently fluctuated around 30 000 pairs from 1993/1994 to 2005/2006 (Crawford et al. 2007). On account of this large decrease it was deemed prudent to ascertain whether the six colonies still dominate South Africa’s population and hence whether it is valid to use them to assess the conservation status of the population. In 2010–2014, the six localities supported 82% of the South African population (Table 1). This indicates that, as South Africa’s overall population decreased, the relative importance of localities other than the original ‘big six’ increased. At the same time, mean colony size decreased, although not significantly because of a wide range of colony sizes and a standard deviation more than twice the mean in both 1977–1981 and 2010–2014. In the latter period, eight localities each held >1 000 pairs of Cape cormorants and together they accounted for 91% of South Africa’s population. Lambert’s Bay was no longer a major contributor, but the five southern members of the ‘big six’ retained their dominant status and they were joined by Schaapen Island, Robben Island and Stony Point (Table 1).

The regional status of Cape cormorants in South Africa may be affected by the increased relative importance of other breeding localities. Smaller colonies were seldom counted between 1982 and 2011, but 97 000 pairs bred at the big six localities in 1988 (Crawford et al. 2007), whereas the overall population was 57 000 pairs in 2010–2014. This represents a minimum decrease of 40 000 pairs (41%) over a period of 24 years. If the generation time (T) for Cape cormorants is calculated as A + 1 / (1 – S), where A is age of first breeding and S is adult survival (BirdLife International 2000), values of A = 3 years (a younger age at first breeding of two years may apply when food is plentiful; Crawford et al. 2001) and S = 0.84 per annum (Crawford et al. 1992a) yield an estimate of T = 9.25 years,
which is slightly longer than the 8.67 years used by Cook (2015). The minimum 41% decrease over 2.6 generations then equates to 16% per generation or 48% in three generations, just below the 50% requirement for classification as Endangered in terms of the IUCN (International Union for Conservation of Nature) criterion A2 (BirdLife International 2000). Because numbers breeding at localities other than the big six were not accounted for in 1988 and the actual overall decrease between 1988 and 2010–2014 is unknown, but >41%, the assessment of Endangered by Cook (2015), which was based on comparative information, is appropriate and should be retained. However, in future it would be desirable to base assessments of status on information from a greater number of breeding localities.

The novel feeding strategies (scavenging and large groups feeding in coastal lakes) observed in 2014 and 2015 indicate some flexibility in the foraging behaviour of Cape cormorants (see also Shelton et al. 1978; Hockey et al. 2005; Ryan et al. 2010; Hamann et al. 2012). On 7 September 1989, at Kalk Bay (near Simon’s Town; Figure 1), Cape cormorants scavenged on offal discarded by handline boats (BMD pers. obs.), the only known previous observation of the species feeding by scavenging prior to the recent observations of bait (saury) being taken from handlines in 2014. *Scomberesox saurus* is found around South Africa and often fed upon by Cape gannets, but seldom taken naturally by Cape cormorants, which generally do not forage as far offshore as gannets (Hockey et al. 2005); *Cololabis saira* is imported bait. Scavenging can help to offset temporary shortages of preferred prey. However, taking bait from handline fisheries comes at a cost in terms of injury and mortality, requires mitigation through adequate hook-weighting and education of fishers, and scavenged food often has a lower nutritional value than natural prey (e.g. Grémillet et al. 2008). Although Cape cormorants often forage in coastal wetlands, this is usually in small numbers (Hockey et al. 2005). Similarly to the use of coastal lakes in 2014 and 2015, there was a large-scale influx of Cape cormorants into several Eastern Cape estuaries in June/July 1994, when anchovy and sardine were scarce in the vicinity and many Cape cormorants died from starvation (Martin 1994).

In addition to their somewhat plastic foraging behaviour, Cape cormorants readily adjust their breeding habitat. For example, after artificial platforms were erected in north-central Namibia, many Cape cormorants bred on them (Cooper et al. 1982), thereby increasing their proximity to shoals of sardine (Crawford 2007). However, although Cape cormorants have a relatively long foraging range compared to that of other species of cormorants, it is much shorter than that of Cape gannets (c. 300 km, Lewis et al. 2006; Pichegru et al. 2007) and successful breeding by Cape cormorants depends on the reliable occurrence of pelagic fish schools within their foraging range (Ryan et al. 2010). A possible measure to counter the recent decrease of Cape cormorants would be the provision of suitable breeding habitat (such as platforms) for the species between Dyer Island and islands in Algoa Bay. In recent years, along this coastline substantial proportions of South Africa’s populations of anchovy and sardine have resided in summer (Roy et al. 2007; Coetzee et al. 2008), but there are no sizeable islands. This has restricted breeding by Cape cormorants to beaches, cliffs and stacks, and until now colony sizes have been <1 000 pairs. If carefully planned and successfully implemented, the provision of artificial habitat would not only improve the conservation status of one of the Benguela system’s threatened, endemic seabirds, but could also have socio-economic benefits, for example through increasing ecotourism opportunities in the region and providing a harvest of seabird guano, a sought-after natural fertiliser (e.g. Crawford and Shelton 1978; Crawford et al. 2007). It should be noted, however, that South Africa’s south coast has higher rainfall than Namibia’s coast, so the potential for guano to be washed away by rain is higher than in Namibia.

In the interim, it is important that attempts be made to ensure sufficient food around extant colonies, especially Dyer Island, which holds >50% of South Africa’s population (Cook 2015), for example by reducing fishing effort near to colonies (e.g. Sherley et al. 2015). It is also necessary that existing colonies be secured from undue disturbance by humans; for example, in the Wilderness/Sedgefield area there has been an increase in various forms of paragliding around sea cliffs used by Cape cormorants for breeding.

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