Foraging behaviour of bank cormorants in Namibia: implications for conservation

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ABSTRACT: We studied the foraging and diving behaviour of male bank cormorants *Phalacrocorax neglectus* at Mercury Island, Namibia, during the 2007–2008 breeding season. The island hosts the world's largest breeding colony of this endangered species. Population numbers are currently stable at Mercury Island, whereas numbers at other colonies in Namibia are decreasing, including those at formerly important colonies. This trend is presumably due to reduced food availability. At Mercury Island, bank cormorants foraged inshore (ca. 2 km off the coast) in close vicinity to their breeding site (ca. 3 km off the colony) and dived to an average depth of 30 m. Diet at Mercury Island was dominated by demersally occurring pelagic goby *Sufflogobius bibarbatus*. Our findings suggest that bank cormorants are benthic feeders along their entire range and that their foraging behaviour in Namibia does not differ from that suspected in South Africa. Further studies, extending to other breeding sites, are needed to explain the different population trends and how these may be influenced by food availability. The identification of important foraging sites will play a crucial role in the management of Namibia's first Marine Protected Area and will contribute towards the protection of this species.

KEY WORDS: Bank cormorant · *Phalacrocorax neglectus* · Namibia · Foraging · Benthic diving · Endangered species

INTRODUCTION

Bank cormorants *Phalacrocorax neglectus* are endemic to the Benguela Upwelling System and are listed as endangered (Kemper et al. 2007, IUCN 2008). Mercury and Ichaboe Islands in Namibia, near the northern extreme of the species' range (Fig. 1), support 70 to 80 % of the species (Kemper et al. 2007), while other breeding localities in Namibia and South Africa hold the remainder in smaller colonies (Kemper et al. 2007, Crawford et al. 2008a; Fig. 1). Since the 1990s, numbers in South Africa have shown a slight overall decrease (Crawford et al. 1999) but an increase at some colonies since 2000 (Crawford et al. 2008a), whereas bank cormorants breeding in Namibia

declined by 68 % between 1993 and 1998 (Roux & Kemper 2009). Numbers at Ichaboe Island, previously the world's largest breeding colony, have not recovered and the Namibian population continues to decrease (Kemper et al. 2007). The main reason for the overall population decline is thought to be food shortage (Crawford et al. 1999, 2008a), but other factors, e.g. predation and displacement by seals, also play an important role (Crawford et al. 1989, du Toit et al. 2004).

Since 1999, Mercury Island has hosted the world's largest breeding colony with ca. 1840 breeding pairs during peak breeding (Kemper et al. 2007). At Mercury Island, numbers have increased since the late 1990s and have been stable since 2004. Namibia's first
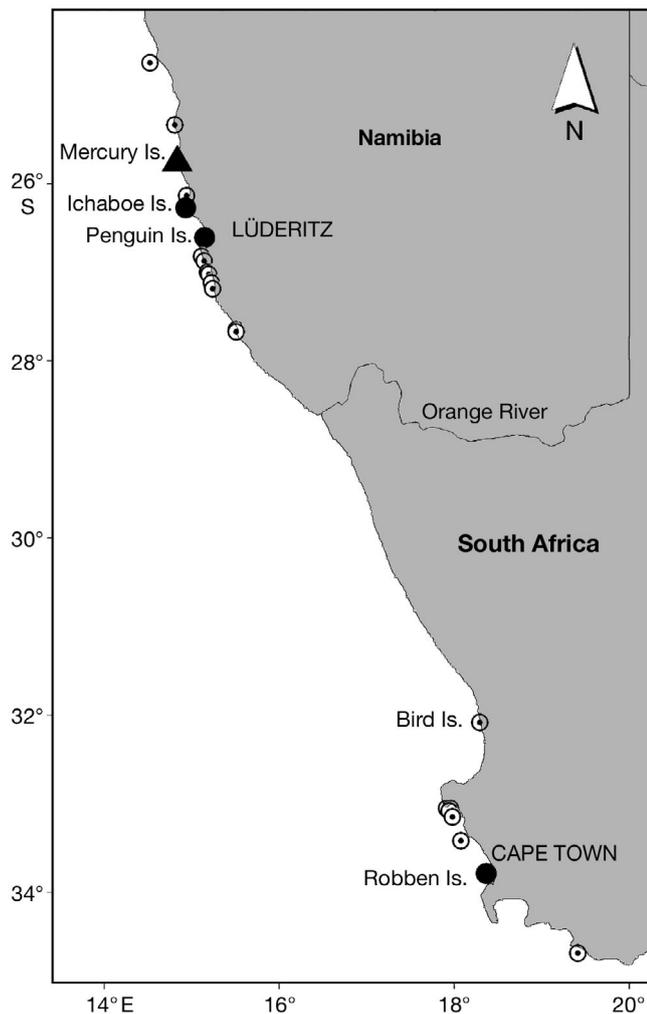
Fig. 1. *Phalacrocorax neglectus*. Breeding sites of bank cormorants along the Namibian and South African coast. ⊙: colonies with <100 breeding pairs; ●: colonies with 100 to 300 breeding pairs; ▲: indicates Mercury Island with >1800 breeding pairs (data from Kemper et al. 2007)

Marine Protected Area, the Namibian Islands' Marine Protected Area (NIMPA), was proclaimed in 2009 (Government Gazette notice no. 4210 of 16 February 2009) and encompasses all breeding sites for bank cormorants in Namibia. Its chief aim is the protection of a number of threatened species, as well as key breeding and foraging habitats along Namibia's southern coast. The identification of foraging areas of bank cormorants and other threatened bird species in the NIMPA is essential for the successful implementation of management plans and, ultimately, the conservation of this species.

Few studies have investigated the foraging and diving behaviour of bank cormorants (Siegfried et al. 1975, Cooper 1985b, Wilson & Wilson 1988); these used different methods, making comparisons difficult. A better understanding of bank cormorant foraging ecology, especially regarding differences between breeding localities, is crucial for their protection. Timing of breeding (Crawford et al. 1999) and colony sizes (Crawford et al. 1999, Kemper et al. 2007) vary across bank cormorants' breeding range and differences are also assumed to exist in their foraging and diving behaviour (Crawford et al. 1985, Hockey et al. 2005). Bank cormorants have been observed feeding inshore and in close vicinity to their breeding sites (Siegfried et al. 1975, Cooper 1985b). Bank cormorants in South Africa feed mainly on Cape rock lobster *Jasus lalandii*, thus feeding at the sea bottom, while the main prey for this species breeding in Namibia is pelagic goby *Sufflogobius bibarbatus* (Cruickshank et al. 1980, Cooper 1985b, Crawford et al. 1985, 2008a). This has led to the assumption that bank cormorants feed pelagically, in the water column, in Namibian waters (Crawford et al. 1985, Hockey et al. 2005).

The present study investigated the diving and foraging behaviour and foraging areas of breeding bank cormorants at Mercury Island, Namibia, using data logger technology and nest observation data. We examined whether bank cormorants in Namibia are actually pelagic feeders in contrast to their conspecifics in South Africa (Crawford et al. 1985), identified important foraging areas and offer potential reasons for the positive population trends at Mercury Island.

MATERIALS AND METHODS

Study site. The study was carried out at Mercury Island, Namibia (25° 43′ S, 14° 50′ E; Fig. 1), during the 2007–2008 breeding season. Nest observations and data logger deployment took place between 14 February and 6 March 2008.

Nest observations. Nest observations were carried out from vantage points at different breeding colonies around the island. Between 5 and 13 nests were observed at the same time, recording departure and arrival times of individual birds. We did not determine the sex of the birds but nest status was noted (nests with eggs or chicks or birds building the nest). Observation periods lasted between 01:15 and 03:45 h; incomplete trips (i.e. birds not observed departing or returning) were excluded. We distinguished trips made for the purpose of foraging or the collection of nest material by trip duration. Birds observed returning with nest material usually did not spend more than 10 min away from the nest site (see 'Results'); we therefore defined foraging trips as those longer than 10 min. Daylight periods were defined as 06:30 to 20:00 h.

Data logger deployment. We used a geographical positioning system MiniGPS (earth&OCEAN Technologies) weighing 29 g with dimensions of $46.5 \times 32 \times 18.5$ mm (length × width × height). MiniGPS were set to record positional information every minute; accuracy in this mode is ca. 10 m (65% of all fixes with accuracy of <10 m in intermittent mode; earth& OCEAN Technologies pers. comm.). The second data logger type used was the temperature-depth recorder PreciTD (earth&OCEAN Technologies), weighing 23 g and with a diameter of 19 mm and a length of 80 mm. These devices were set to measure pressure (i.e. water depth) and temperature every second; in most cases memory size (2 MB) allowed for data storage of the entire deployment period. Devices were attached to the center tail feathers using Tesa® tape, placed either on top or underneath the tail (MiniGPS and PreciTD, respectively). Devices used in the present study weighed less than 1.5% of the bird's body mass and only one device was used on each individual.

Devices were deployed on 17 breeding bank cormorants. Birds were raising 1 to 3 chicks of different ages (few days to several weeks of age) and only one partner of each nest was handled. We used MiniGPS data loggers on 7 and PreciTD data loggers on 10 birds. We sexed the birds according to body size, males being the larger member of the pair (Cooper 1985a). Devices were deployed on 15 males (average ±SD mass = 2.04 ± 0.18 kg) and 2 females (both weighing 1.74 kg).

Birds were captured at their nest sites using a hooked pole. Weighing and logger deployment took less than 8 min, after which the birds were returned to their nests. Data loggers were removed after 1 to 3 d, except in one case where a female (carrying a MiniGPS device) did not return and abandoned her nest. After the departure of the partner 2 d later, the chicks were transferred to another nest where they were successfully raised to fledging.

Data analysis. We present data for 13 males successfully equipped with data loggers (1 MiniGPS and 1 PreciTD did not yield data); the data from the 1 female carrying a PreciTD device are only used for comparison. Data were obtained from 8 male birds equipped with PreciTD loggers. For 1 bird no pressure data were recorded, so dive data for 7 birds are presented. The number of dives for the eighth bird was determined using the temperature signal. Trip duration data were available for all 13 birds. An ANOVA was used to compare trip durations for different device types and chick-rearing birds observed in the colony using the open source software package R 2.4.1 (www.r-project.org).

Positional data obtained from MiniGPS devices were plotted and analysed using ArcView 3.2 (ESRI). Only trips with more than one position obtained away from the colony were included. When only one fix was recorded away from the colony, this was not considered a trip but rather inaccurate positioning. Adaptive kernel analysis using ArcView 3.2 was used to calculate the overlap of foraging areas between individual birds, based on the 50% kernel volume contour (De Solla et al. 1999, Wood et al. 2000).

Consecutive positions that showed that the bird had travelled <50 m min^{-1} were defined as foraging areas. This value was chosen according to the frequency distribution of distance travelled between fixes, of which 50% were <50 m min^{-1}. The activity recorded using PreciTDs (see 'Results: Diving') underlines this definition.

Temperature and pressure signals of birds equipped with PreciTD data loggers were used to estimate trip durations and at-sea activities, such as surface periods, flying and diving, using the methods devised by Wilson et al. (1995) and Garthe et al. (1999). High and relatively stable temperatures indicated the birds' presence in the colony, while departures to sea were characterized by a sudden change in the temperature signal which fluctuated until the bird landed on the water. Surface periods showed a stable and relatively low temperature signal and water temperatures were confirmed by measurements at the island. Dives were defined by the pressure signal as well as by a drop in temperature (used as a proxy for the device with the
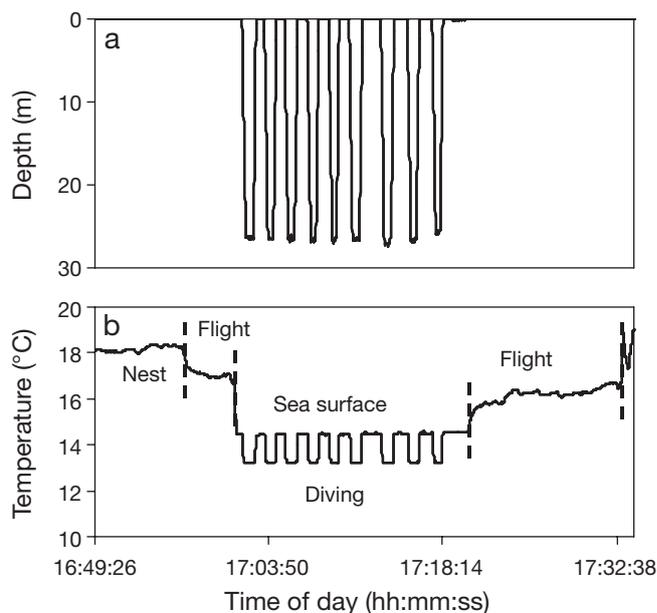

Fig. 2. *Phalacrocorax neglectus*. Example of the (a) depth and (b) temperature signal recorded during a single foraging trip using PreciTD data loggers. Different activities identified by the temperature signal are pointed out in (b); sea surface refers to the time the bird spent at the sea surface between and after dives

malfunctioning pressure signal; Fig. 2). Post-dive intervals (PDI) were defined as the surface time following each dive which ended when the bird either dived again or was presumed flying (see Tremblay et al. 2005). Dives were defined as being >1 m depth and a sequence of dives not interrupted by flying was defined as a dive bout. Bottom time was defined as the period of a dive when the vertical velocity of the bird was <0.2 m s^{-1} after linear descent and before linear ascent phases. Dive sequences in which successive maximum dive depths were within 10% of each other were analysed for potential bottom feeding (following Tremblay & Cherel 2000). Time spent underwater was calculated as the sum of all dive durations per trip. Correlations between trip duration, time spent at the surface, time spent under water, number of dives and flight time were tested using a linear model in R 2.4.1. One trip with an untypically long surface period after the last dive (>1 h) was excluded from the correlation analysis. Individual differences in dive duration and dive depth were tested using a permutation test as per Oatley & Underhill (2001).

To determine possible foraging areas of birds equipped with PreciTD devices (thus not yielding any information about their locations at sea), distances were calculated by multiplying the average flight speed calculated from MiniGPS devices during periods of commuting, equalling 50 km h^{-1} (13.8 m s^{-1}), with flight times between departure from the nest and the first activity at sea (floating or diving) and between the last activity and the return to the nest. Possible locations of these foraging areas and the corresponding dive depths were then compared to bathymetric data (South African Navy Chart SAN 110) to evaluate bottom diving.

RESULTS

Foraging trip length

In 92.2% of all trips observed (n = 86), birds returning with nest material stayed away for <10 min. We therefore defined trips >10 min in duration as foraging trips. Foraging trips of chick-rearing birds observed in the colony had a mean (±SD) duration of 41.4 ± 19.8 min (n = 46, range = 12 to 115 min; Table 1). Mean trip durations did not differ significantly between different data logger types nor between data logger and observation-derived data (ANOVA, $F_{2,157}$ = 1.465, p = 0.234; Table 1). The mean foraging trip duration for all trips combined was 39.3 ± 17.4 min (n = 144 trips).

Birds deployed with data loggers averaged 4 trips per day (mean ± SD = 3.8 ± 1.4; considering only days with complete data logger coverage). Birds made a

Table 1. *Phalacrocorax neglectus*. Trip durations of foraging trips (>10 min) of chick-rearing bank cormorants at Mercury Island, Namibia, in February and March 2008. Birds equipped with PreciTD and MiniGPS data loggers included only male birds; sexes of birds observed in the colony are unknown. Duration values were obtained from nest observations for undeployed birds and from recorded trip durations for birds deployed with data loggers

Data source	No. of trips	Trip duration Mean ± SD	Range
Observations	46	41.4 ± 19.8	12–115
PreciTD (n = 8 birds)	64	39.7 ± 17.8	17–120
MiniGPS (n = 5 birds)	34	35.5 ± 12.3	13–62

maximum of 7 trips for nest material in one day. Total time at sea per day averaged 131 ± 45 min (n = 16 complete days of 11 birds, range = 68 to 228 min), thus only 16.2% of the daylight period was used for foraging. The average time between consecutive foraging trips (ignoring short trips for nesting material) was 144 ± 73 min (n = 64, range = 3 to 344 min). The earliest trip in the morning started 14 min after local sunrise at 06:44 h and the latest return of a bird to the colony took place at 19:34 h, 26 min before local sunset. No activity was recorded during the night.

The mean (±SD) trip duration of 15 trips made by the single female was 44.7 ± 16.7 min. This bird spent 209 and 269 min (25.8 and 33.2% of the daylight period) at sea on 2 consecutive days. Foraging took place between 06:57 and 18:21 h.

Foraging areas

The 5 birds successfully equipped with MiniGPS data loggers flew in a southwesterly direction to forage (Fig. 3). Three of the birds additionally flew in a northerly and northwesterly direction. Kernel analysis identified areas southwest of the island as well as surrounding the island as being used extensively by all birds combined (Fig. 3f). Individual birds foraged within the same area during several consecutive trips (see Fig. 3); 48% of all trips were within 1 km of the previous ones. Foraging areas during 6 trips recorded for Bird 1 were not farther than 400 m apart (Fig. 3a). Kernel analysis further showed a large overlap of foraging areas between all birds: the 50% kernel volume contour of Birds 1 and 3 overlapped completely; the foraging area of Bird 9 fell within the 50% contour of all other birds; and Birds 9 and 12 used areas very similar to each other, both birds foraging in southerly and northerly directions from the island (Table 2, Fig. 3).

Mean (±SD) maximum distances travelled from the colony were 3.2 ± 2.2 km (n = 33, range = 0.7 to 8.6 km;
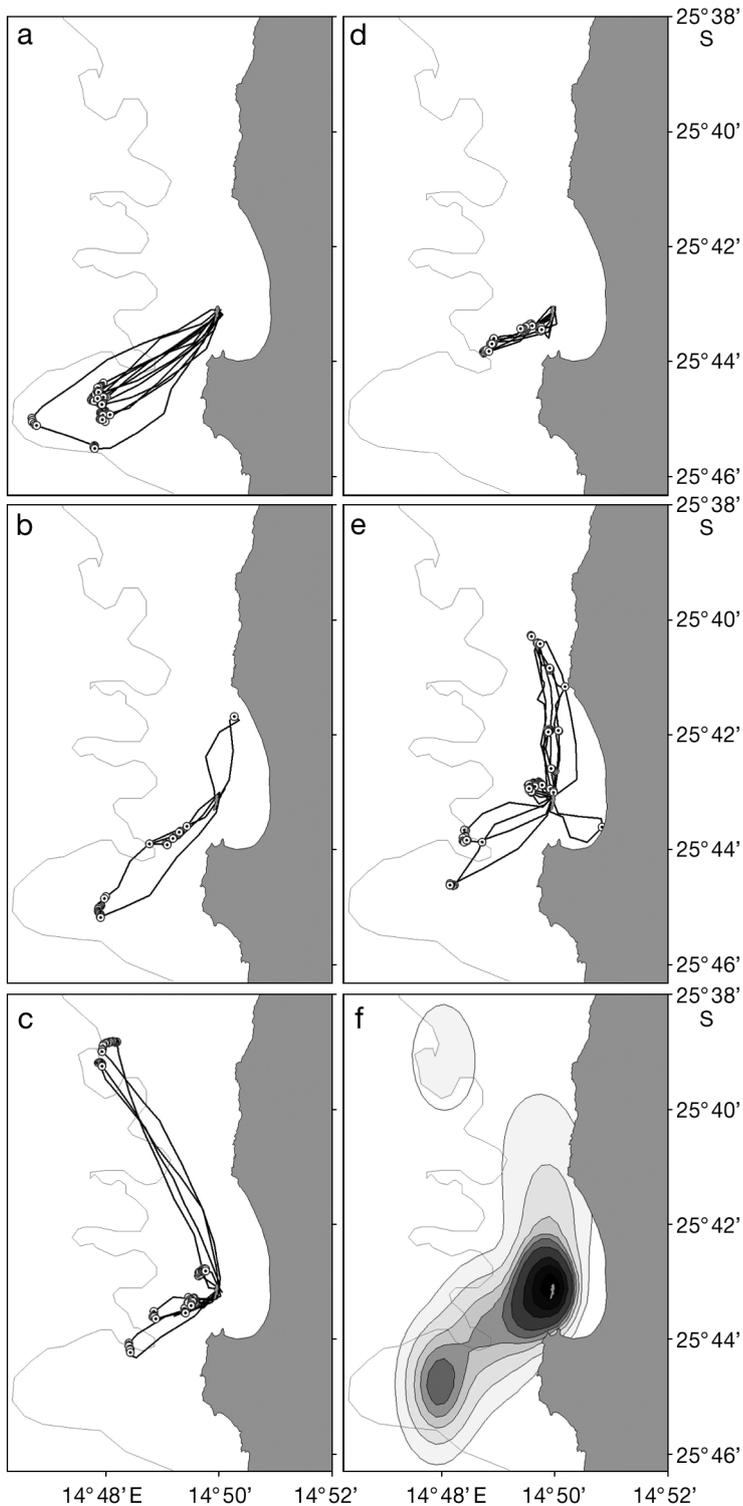
Fig. 3. *Phalacrocorax neglectus*. Foraging tracks and foraging positions (○) of 5 male bank cormorants equipped with MiniGPS data loggers at Mercury Island, Namibia. Tracks shown in (a–e) are by birds no. 1, 3, 6, 9 and 12, respectively. Kernels shown in (f) are of all birds combined over a time period of 2 wk in February and March 2008. Contours give the 10 to 90% kernel volumes, and the contour line in all panels represents the 50 m bathyline

Table 3) and birds travelled a mean distance of 7.8 ± 5.0 km (range = 1.6 to 19.8 km) during foraging trips. Foraging areas (defined by time spent in a certain area, see 'Materials and methods') were located on average 3.1 ± 2.3 km (n = 328 foraging positions for 5 birds; range 0.2 to 8.6 km) away from the colony and 2.1 ± 0.4 km (range 0.1 to 5.0 km) away from the mainland coast. All birds foraged in water < 50 m deep (Fig. 3). Foraging areas of birds carrying PreciTD devices (identified by flight time before and after dives) were located at an average distance of 2.6 ± 1.6 km (range 0.2 to 10.4 km) from the colony.

Diving

Seven male bank cormorants carrying PreciTD data loggers made 448 dives during 48 foraging trips. The mean (±SD) number of dives per trip was 8.48 ± 4.35. Birds dived to a mean depth of 29.9 ± 8.9 m (range = 1.7 to 47.1 m) and the mean duration was 72.4 ± 12.8 s (range = 8 to 115 s; Table 4, Fig. 4). There were no significant differences in dive depth or dive duration between individuals (permutation test, p = 0.157 and p = 0.289, respectively).

Birds dived to similar depths in consecutive dives (see Fig. 2a); the maximum depth of 98.4% of dives was within 10% of the maximum depth of the previous dive, suggesting that birds dived to the sea bottom at depths of ca. 30 and 40 m. Shallow dives (< 10 m) occurred near the beginnings and ends of foraging trips; 5.3% of all dives were shallow. Mean (±SD) bottom time was 31.5 ± 11.0 s (range = 0 to 61 s) and all dives with bottom times shorter than 10 s (3% of all dives) were recorded at the beginning of a dive bout.

Birds floated on the water surface between dives (Fig. 2b); this behaviour made up 47.9 ± 9.6% of the time at sea. PDI had a median duration of 68 s (range = 0 to 1025 s). The maximum dive duration to PDI ratio (mean = 1.38) was recorded for dives lasting between 40 and 50 s, but ratio values of > 1.0 were recorded for dives of up to 80 s, thus for 72% of all dives (Fig. 4b). Less than 10% of all dives were followed by flight activity (mean duration = 80 ± 107 s). Flying was limited to commuting between breeding sites and foraging areas, and birds spent

Table 2. *Phalacrocorax neglectus*. Percentage of area overlap of 50% kernel volume contour of foraging bank cormorants at Mercury Island, Namibia

Bird no.	Bird no.				
	1	3	6	9	12
1	—	100	47.8	29.2	73.8
3	100	—	64.8	31.9	71.7
6	84.9	100	—	36.9	95.9
9	100	100	100	—	100
12	60.5	95	100	31.1	—

22.2 ± 8.9% of their total time at sea flying. Trip duration was most strongly correlated with the time spent floating at the surface between and after dives ($r^2 = 0.85$, $F_{1,62} = 364.2$, p < 0.001; n = 64 trips of 8 birds), followed by the time spent underwater ($r^2 = 0.56$, $F_{1,46} = 59.5$, p < 0.001; n = 48 trips of 7 birds) and the number of dives per trip ($r^2 = 0.4$, $F_{1,62} = 41.7$, p < 0.001; n = 64 trips of 8 birds). Trip duration was also positively correlated with the time spent commuting between the colony and the foraging area, e.g. flying time ($r^2 = 0.31$, $F_{1,62} = 27.97$, p < 0.001; n = 64 trips of 8 birds).

The only female from which we obtained data dived more frequently (mean ± SD = 13.3 ± 8.4 per trip) than male birds, but mean diving depth and dive duration were similar to those of male birds (27.2 ± 8.2 m and 64. 3 ± 14.8 s). The maximum depth of 75% of dives was within the 10% of the previous maximum depth and the female cormorant dove to <10 m in 13.5% of all dives. Additionally, the female flew for longer periods (185 ± 113 s) between dive bouts. According to time spent flying before and after diving, the female bank cormorant foraged at an average distance of 2.5 ± 1.6 km (range = 0.7 to 7.4 km) from the colony.

DISCUSSION

Food availability is an important factor influencing seabird population sizes (e.g. Weimerskirch 2001). Poor food availability may directly affect breeding success (Aebischer 1986, Rindorf et al. 2000, Lewis et al. 2001, Wanless et al. 2005, 2007, Crawford et al. 2006), lead to emigration (Oro et al. 2004, Crawford et al. 2008b) and, under extreme circumstances, even cause adult mortality (Hays 1986, Duffy 1989, Boersma 1998). Food scarcity is suspected to pose a significant risk to a number of threatened seabird species in the Benguela system, including bank cormorants (Crawford et al. 1999, 2008a, Crawford 2007, Kemper et al. 2007). Studying the foraging behaviour of bank cormorants at Mercury Island might help to explain why it is the largest breeding colony and why its population is stable to increasing compared to other breeding sites. However, the lack of comparative data from other breeding sites on foraging behaviour and diet composition of bank cormorants makes answering these questions difficult.

Frequent trips of short duration and little time spent at sea indicate good prey availability close to the breeding colony (Cooper 1985b, Wanless et al. 1995,

Table 4. *Phalacrocorax neglectus*. Diving parameters for male bank cormorants at Mercury Island, Namibia, equipped with PreciTD data loggers in February and March 2008. Given are mean values (±SD) for all trips (n) during the time of logger recording (logger time) for each bird. nd: no data

Bird no.	n	Logger time (hh:mm:ss)	Trip duration (min)	Dives trip^{-1}	Dive depth (m)	Dive duration (s)
2	5	31:27:00	54.2 ± 8.4	9.2 ± 1.8	39.3 ± 2.2	86.7 ± 3.9
4	3	29:57:00	54.3 ± 5.1	16.3 ± 5.5	25.7 ± 0.6	69.2 ± 1.8
5	6	36:53:00	41.8 ± 15.7	10.7 ± 6.0	26.8 ± 2.6	65.5 ± 7.9
10	11	70:51:00	26.7 ± 8.4	8.5 ± 2.7	23.7 ± 7.1	65.5 ± 9.6
11	2	68:12:00	41.5 ± 7.8	15.0 ± 2.8	22.8 ± 2.7	59.1 ± 0.4
13	12	71:59:00	33.0 ± 13.8	8.4 ± 4.7	33.8 ± 9.0	80.8 ± 13.7
14	16	71:48:00	25.4 ± 7.5	5.6 ± 1.5	nd	nd
17	10	49:23:00	41.5 ± 28.2	7.8 ± 4.3	32.4 ± 11.0	71.5 ± 13.1

Table 3. *Phalacrocorax neglectus*. Foraging trip parameters of male bank cormorants at Mercury Island, Namibia, equipped with MiniGPS data loggers in February and March 2008. Given are mean values (±SD) for all trips (n) during the time of logger recording (logger time) for each bird

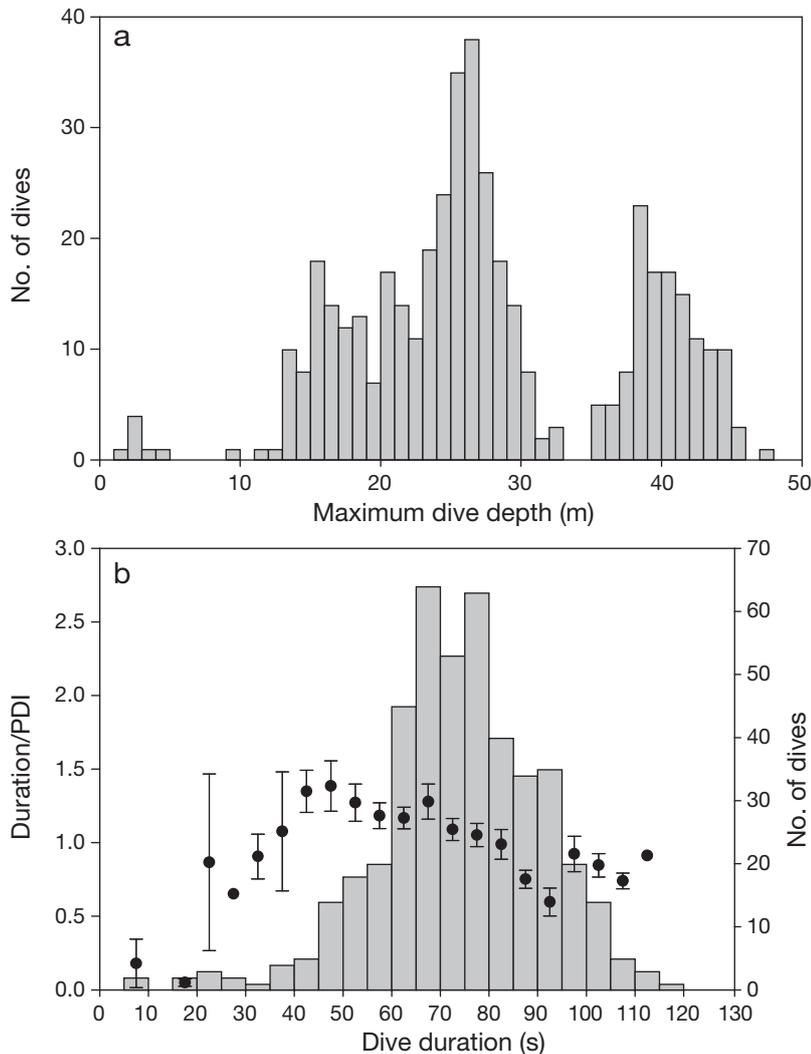| Bird no.	n	Logger time (hh:mm:ss)	Trip duration (min)	Foraging range (km)	Distance travelled (km)	Foraging positions	
						Distance to colony (km)	Distance to coast (km)
1	6	27:46:00	41.0 ± 11.6	5.1 ± 0.8	12.5 ± 2.6	4.3 ± 0.6	3.2 ± 0.6
3	3	29:52:00	42.7 ± 16.3	3.5 ± 1.5	8.7 ± 3.1	4.3 ± 1.4	2.6 ± 0.8
6	8	53:30:00	39.1 ± 12.6	3.3 ± 3.2	8.0 ± 7.1	3.4 ± 3.3	2.2 ± 1.2
9	5	25:58:00	24.4 ± 2.8	1.8 ± 0.7	4.5 ± 1.4	1.5 ± 0.7	1.2 ± 0.4
12	11	71:58:00	34.9 ± 10.6	2.7 ± 1.9	6.5 ± 4.3	2.3 ± 1.5	1.7 ± 0.5

Fig. 4. *Phalacrocorax neglectus*. Frequency distribution of (a) maximum dive depth (m) and (b) dive duration to post-dive interval (PDI) ratio (●; mean ± SD) and dive duration (s, bars) for male bank cormorants at Mercury Island, Namibia (n = 448 dives)

We therefore may have underestimated the number of foraging trips. In addition, we may have introduced a bias in our results by only including male bank cormorants in the data logger analyses. Sex differences in foraging and diving behaviour, as well as colony attendance patterns, have been observed in several cormorant species (Bernstein & Maxson 1984, Kato et al. 1992, 2000, Wanless et al. 1995, Watanuki et al. 1996, Cook et al. 2007), including bank cormorants (Cooper 1985b). Future studies might examine whether there are sex differences in foraging and breeding behaviour of bank cormorants and how these are related to size and weight differences between males and females.

Frere et al. (2008) defined foraging areas of cormorants by single positions where repeated dives were made at the same location. At Mercury Island, bank cormorants equipped with MiniGPS fed inshore and close to the colony, similar to the pattern observed at other breeding sites (Siegfried et al. 1975, Cooper 1985b). Flying was mostly restricted to commuting between the island and the foraging area and seldom occurred between dives. Individual birds showed strong foraging site fidelity, repeatedly visiting the same area southwest of the colony; individual birds returned to almost the exact spot in consecutive trips. This phenomenon has been reported for pelagic-feeding seabirds (e.g. gannets, Hamer et al. 2001; penguins, Watanuki et al. 2003; kittiwakes, Irons 1998) and benthic-feeding seabirds (e.g. penguins, Mattern et al. 2007; cormorants, Grémillet et al. 1999, Quintana 2001, Watanuki et al. 2004). Shags are suspected to memorize special characteristics of the environment and of the sea bottom topography in order to recognize efficient feeding areas in consecutive trips (Cook et al. 2006).

Bank cormorants at Mercury Island foraged almost exclusively at depths of ca. 30 and 40 m, which, taking into account the consistency of dive depth and bottom time duration in accordance with local bathymetry, indicates a benthic foraging behaviour (see Grémillet et al. 1998, 1999). Bottom-feeding has been documented for bank cormorants in South Africa feeding on rock lobster (Cooper 1985b, Williams 1987, Wilson & Wilson 1988). Erroneously, bank cormorants in Namibia have been assumed to feed pelagically, owing to

Quintana 2001). Compared to foraging behaviour recorded for bank cormorants at Bird and Ichaboe Islands through direct observations (Cooper 1985b), male bank cormorants equipped with data loggers at Mercury Island undertook slightly more foraging trips per day (4 versus 3.5), with shorter trip lengths (38 versus 68 min), and spent less time at sea per day (134 versus 240 min). Trip duration in the present study was positively correlated with time spent at the surface between dives, number of dives and time spent underwater. Therefore, an increase in the time spent at sea was the result of increased foraging activity and only to a lesser extent due to increased flying time. Although we excluded trips shorter than 10 min from the analyses, some short trips, deemed to be nest material collection trips, included several deep dives (up to 29 m).

the high percentage of pelagic goby in their diet (Cruickshank et al. 1980, Cooper 1985b). Although juvenile pelagic goby are found in shoals in midwater, adult individuals occur in a more dispersed manner on the seafloor (Cruickshank et al. 1980, Melo & Le Clus 2005). Grémillet et al. (1998) showed that individual cormorants may show flexible diving behaviour, thus being able to use both pelagic and benthic resources. Nevertheless, pellets of indigestible material regurgitated by bank cormorants at Mercury Island indicate that their diet is dominated by adult pelagic gobies of ca. 7 to 12 cm total length (Ministry of Fisheries and Marine Resources [MFMR], Namibia unpubl. data). Other prey species, such as sole (Soleidae), klipfish (Clinidae) and lobster, found in bank cormorant pellets at Mercury and Ichaboe Islands (MFMR unpubl. data) confirm our findings that bank cormorants in Namibia feed benthically. Although pellets may underrepresent certain prey types (Brown & Ewins 1996), they are a useful tool for identifying the diet composition in cormorants (Duffy & Laurenson 1983).

Our results indicate that bank cormorants may show benthic feeding behaviour throughout their range and that birds in Namibia are not necessarily pelagic feeders as previously stated by Crawford et al. (1985) and Hockey et al. (2005). Differences in prey composition may explain the longer dive durations observed in the present study compared to those reported from South Africa by Cooper (1985b) using observational data, which would rather overestimate dive duration. Bank cormorants in South Africa mainly feed on rock lobster (Crawford et al. 2008a). Birds preying on lobster presumably obtain only one prey item per dive, with which they often surface in order to shake off the legs (Avery 1983). Birds feeding on pelagic goby are able to catch and swallow several fish during a single dive, thus also reducing the risk of losing prey due to kleptoparasitism (Avery 1983). PDI were short and a high percentage of dive durations had a maximum dive duration to PDI ratio of >1.0. Longer surface times needed for handling lobsters would lead to an increase of PDI and less efficient foraging in terms of the percentage of time spent diving per foraging trip.

Pelagic goby is of relatively low energetic value (Cruickshank et al. 1980, K. Ludynia unpubl. data), but seems to be an abundant food source around Mercury Island, where it is also the dominant prey species in the diet of breeding African penguins (Crawford et al. 1985, Ludynia 2007, MFMR unpubl. data). Pelagic goby also seems to be a predictable food source as indicated by bank cormorants repeatedly foraging in the same area in the present study. Predictability of food sources may compensate for poor energy content (Grémillet et al. 2004). Bank cormorants at Ichaboe Island also feed predominantly on pelagic goby

(Cooper 1981, Crawford et al. 1985, Duffy et al. 1987, MFMR unpubl. data), but numbers of bank cormorants there have declined sharply since the early 1990s (MFMR unpubl. data). The causes for the different population trends are unclear, but are likely to be related to local predictability and abundance of prey. Numbers of breeding bank cormorants have decreased in areas with reduced abundance of rock lobster in South Africa (Crawford et al. 2008a), and most colonies in South Africa do not fall within the distribution of pelagic goby (Cruickshank et al. 1980). Studies on inter-island movement as well as breeding success of bank cormorants at Namibian and South African breeding sites are currently being undertaken (MFMR unpubl. data, R. Sherley unpubl. data). Further studies on the foraging ecology of bank cormorants are needed at all main breeding sites. The results of the present study, namely the identification of key foraging areas and diving behaviour for birds at Mercury Island, will be incorporated into the NIMPA's management plans. Possible management measures include a ban on lobster fisheries within the area to reduce risks of entanglement of benthic diving birds in traps (see Cooper 1985b), as well as measures to secure prey availability around breeding sites.

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