On a wing and a prayer: the foraging ecology of breeding Cape cormorants

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Abstract

The Cape cormorant *Phalacrocorax capensis* is unusual among cormorants in using aerial searching to locate patchily distributed pelagic schooling fish. It feeds up to 80 km offshore, often roosts at sea during the day and retains more air in its plumage and is more buoyant than most other cormorants. Despite these adaptations to its pelagic lifestyle, little is known of its foraging ecology. We measured the activity budget and diving ecology of breeding Cape cormorants. All foraging took place during the day, with 3.6 ± 1.3 foraging trips per day, each lasting 85 ± 60 min and comprising 61 ± 53 dives. Dives lasted 21.2 ± 13.9 s (maximum 70 s), attaining an average depth of 10.2 ± 6.7 m (maximum 34 m), but variability in dive depth both within and between foraging trips was considerable. The within-bout variation in dive depth was greater when making shallow dives, suggesting that pelagic prey were targeted mainly when diving to < 10 m. Diving ecology and total foraging time were similar to other cormorants, but the time spent flying (122 ± 51 min day^{-1}, 14% of daylight) was greater and more variable than other species. Searching flights lasted up to 1 h, and birds made numerous short flights during foraging bouts, presumably following fast-moving schools of pelagic prey. Compared with the other main seabird predators of pelagic fish in the Benguela region, Cape gannets *Morus capensis* and African penguins *Spheniscus demersus*, Cape cormorants made shorter, more frequent foraging trips. Their foraging range while feeding small chicks was 7 ± 6 km (maximum 40 km), similar to penguins (10–20 km), but less than gannets (50–200 km). Successful breeding by large colonies depends on the reliable occurrence of pelagic fish schools within this foraging range.

Introduction

Cormorants are foot-propelled pursuit divers that reduce their buoyancy, and hence the energetic cost of diving, by limiting the amount of air trapped in their feathers (Wilson *et al.*, 1992). This reduces the insulation of their plumage while diving, typically limiting cormorants to relatively short, intense foraging bouts (Grémillet & Wilson, 1999). At their extreme northern limit, great cormorants *Phalacrocorax carbo* only feed for about 10 min each day in winter (Grémillet *et al.*, 2001). Although European shags *Phalacrocorax aristotelis* spend up to 7 h day^{-1} foraging (Daunt *et al.*, 2006), all cormorants roost ashore at night, limiting them to coastal waters (Nelson, 2005). The Cape cormorant *Phalacrocorax capensis*, endemic to the Benguela upwelling region, is unusual among cormorants in feeding up to 80 km offshore, and may rest at sea for protracted periods (Siegfried *et al.*, 1975). Although it is a versatile

forager, ranging from estuaries and shallow tidal pools to far offshore, it feeds primarily on pelagic schooling fish (Rand, 1960; Crawford & Dyer, 1995) and has structural adaptations to its head and neck for catching fast-moving, pelagic prey (Burger, 1978). Compared with the great cormorant, it is considerably more buoyant (Wilson *et al.*, 1992).

The land-based component of the breeding biology of Cape cormorants has been well studied (Berry, 1976). Most breed in large colonies that depend on a reliable source of pelagic fish (Crawford & Dyer, 1995). Cape cormorant numbers have decreased in the last few decades linked to decreases in the abundance of pelagic fish, and exacerbated by outbreaks of avian cholera and increased predation (Crawford *et al.*, 2007). Given the impacts of commercial fisheries on pelagic fish, it is important to understand the foraging ecology of top predators that compete for the same resource. Of the three main seabird predators of pelagic fish,

the foraging ecology of Cape gannets *Morus capensis* and African penguins *Spheniscus demersus* has been studied (e.g. Wilson, 1985; Grémillet *et al.*, 2004; Ropert-Coudert *et al.*, 2004; Petersen, Ryan & Grémillet, 2006; Pichegru *et al.*, 2007), but little is known about the fine-scale foraging ecology of Cape cormorants. Most foraging occurs in water of 5–150 m depth where they use a mix of benthic and pelagic foraging (Duffy, 1989). Observations of dive durations and diving efficiency are confined to birds feeding singly close inshore, presumably on benthic prey (Rand, 1960; Duffy, 1989; Wilson & Wilson, 1988, 1995; Wilson, Wilson & Nöldeke, 1992). It is difficult to obtain diving data for birds feeding on pelagic prey by direct observation because it typically involves flocks of hundreds or thousands of birds (Rand, 1960; Duffy, 1989).

We used activity loggers to study the foraging ecology of breeding Cape cormorants. Comparable studies have been conducted on other cormorants (e.g. Tremblay, Cook & Cherel, 2005; Quintana, Wilson & Yorio, 2007; Wilson *et al.*, 2008), but this is the first study of a species that feeds extensively on pelagic schooling fish and uses aerial searching to locate fish schools. We report how the pelagic lifestyle of Cape cormorants affects their daily activity budgets, and assess whether their diving behaviour differs from other, less buoyant cormorant species.

Methods

The study was conducted on Malgas Island (33°03′S, 17°55′E) off the west coast of South Africa from 26 October to 13 November 2005. Adult Cape cormorants brooding small chicks were caught at their nest between 15:00 and 17:30 h when they were relieved after a brood shift. They were caught with a fine noose on the end of a pole. Males average larger than females, but with extensive overlap (Hockey, Dean & Ryan, 2005), and so birds could not be sexed reliably from measurements. Data loggers were attached to feathers on the birds' lower backs using black Tesa tape, which allows for easy removal without damaging the birds' feathers (Wilson *et al.*, 1997). Handling time was <10 min.

The data logger (M190-D2GT, Little Leonardo, Tokyo, Japan) has a small cross-sectional area (15 mm diameter; length 53 mm) and weighs 17 g, only 1.5% of the minimum mass of breeding Cape cormorants sampled at Malgas Island (1.37 ± 0.12 kg, range 1.13–1.60 kg, $n = 38$). The loggers recorded pressure every 1 s (measuring depth to the nearest 0.1 m) and acceleration on two axes (32 Hz) using tilt sensors to measure dynamic and static acceleration (Ropert-Coudert *et al.*, 2004). The birds were re-caught at their nests 43–68 h later. The loggers had little impact; the birds returned to their nests 2–169 min (median <10 min) after being equipped, and continued to provision their chicks. The frequency and duration of foraging trips were similar to those of birds breeding at islands off the west coast of South Africa during years of good breeding success (median 140 min, range 50–390 min; Duffy *et al.*, 1984).

Acceleration and pressure data were analysed with Igor Pro (Wavemetrics, v. 5.05J, Portland, OR, USA). A dive was recorded when the water depth was >1 m. Vertical descent and ascent rates were calculated in $m\,s^{-1}$ and bottom time was defined as the interval when descent and ascent rates were $<0.25\,m\,s^{-1}$. Because depth is only recorded every 1 s, estimates of dive rate are poor for short dives, and so analyses of dive rate were restricted to dives with descent and ascent periods ≥ 2 s. The effect of maximum dive depth on dive duration, bottom time and descent and ascent rates was calculated for ln-transformed and untransformed data to facilitate comparison with published studies on other cormorants. Serial diving to a particular depth stratum was indicated by assigning a dive that was within 10% of the maximum depth of the preceding dive as an intra-depth zone (IDZ) dive (Tremblay *et al.*, 2005). Dive efficiency was defined as the ratio of dive duration to post-dive recovery periods when there were successive dives (after Dewar, 1924). Post-dive intervals >60 s (1% of the total) were excluded because they probably included other activities (e.g. comfort behaviours). Foraging efficiency has been defined as the ratio of bottom time to total dive time + post-dive intervals (Ydenberg & Clark, 1989). This may be less appropriate for birds that feed extensively on pelagic prey, but we calculated foraging efficiency for dives with bottom times ≥ 2 s and no flight following a dive.

The accelerometer and pressure data together provided a continuous record of bird activity (Fig. 1). Using a low-pass filter to separate static from dynamic acceleration (cf. Kato *et al.*, 2006), we could reconstruct activity budgets. Purpose-written software discriminated between flying (regular vertical heaving at 5–6 Hz), resting on the water (horizontal landing, followed by little activity) and resting on land (alighting with body more vertical) (see also Wilson *et al.*, 2007). It was not possible to tell whether birds on land were at their nests or not. Activity budgets were calculated as a proportion of civil daylight (when the sun is 6° below the horizon: 14:24 h on 4 November; dawn 05:20 h, dusk 19:44 h). Foraging trips were defined as any trip when a bird went to
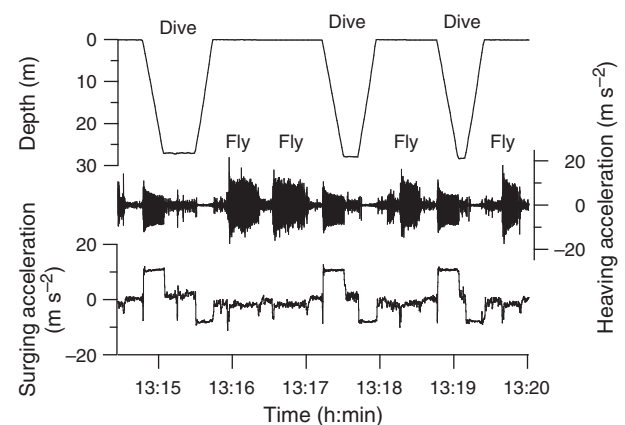
Figure 1 Depth and acceleration traces showing characteristic behaviours of Cape cormorants *Phalacrocorax capensis* during a series of three deep dives with short flights between dives.

sea (Tremblay *et al.*, 2005). This included some very short trips (minimum 2 min, with three dives all < 2 m deep) as well as two trips when no diving took place. Foraging trips were broken into discrete bouts if diving was interrupted by rests or flights > 5 min (Grémillet *et al.*, 1998; Ropert-Coudert *et al.*, 2004). Foraging range was inferred assuming a flight speed of 50 km h^{-1} (Pennycuick, 1987) and that birds return directly to colonies at the end of each foraging trip.

Results

Loggers were deployed on nine Cape cormorants. The batteries died during two deployments, but at least one full day was recorded for all birds (four birds logged for 2 days). Three birds regurgitated prey when recaptured. Bird 1 contained anchovies *Engraulis encrasicolus*, bird 2 anchovies, sardines *Sardinops sagax* and a Cape gurnard *Chelidonichthys capensis* and bird 8 contained anchovies and a southern mullet *Liza richardsonii*. Only the gurnard is a benthic species.

Timing and structure of foraging trips

Despite the ability of some cormorants to forage at low light levels (Grémillet *et al.*, 2005), all foraging took place between dawn and dusk. The first bird departed at 05:02 h (average 07:03 ± 02:39 h, $n = 17$) and diving commenced at 05:22 h (07:58 ± 02:37 h), shortly before sunrise (05:45 h). Diving ceased at 19:36 h (18:12 ± 01:14 h, $n = 17$), shortly after sunset (19:16 h), and all birds returned to the colony by 19:45 h (18:22 ± 1:22 h).

We logged 66 complete foraging trips (mean 7.3 ± 2.5 per bird, range 4–12), lasting 85 ± 60 min (2 min to 5:48 h), with 61 ± 53 dives per trip (range 0–293 dives). Although there was a correlation between trip duration and the number of dives, trip duration explained less than half the variation in the number of dives [number of dives = $0.608 \times$ trip duration (min) + 9.28; $r^2 = 0.471$]. This was largely because of the considerable variability in flight time and the presence of prolonged rests on the water (> 10 min) in 15% of the trips. Two trips to sea lacked any dives: one bird rested on the water for 14 min, and another for 62 min; neither was immediately following deployment. Variance in foraging trip duration was increased by three short trips where foraging lasted < 5 min and had < 5 dives. Excluding these short trips as well as trips with no diving, the average trip duration was 91 ± 58 min (range 8 min to 5:48 h; $n = 61$) with 66 ± 53 dives, but this failed to improve the correlation between the number of dives and the trip duration ($r^2 = 0.430$). Intervals between foraging trips on the same day averaged 01:39 ± 01:32 h (5 min to 5:05 h, $n = 48$); overnight intervals were 12:26 ± 2:59 h (9:33–18:52 h, $n = 16$). Birds also made occasional short trips (5.4 ± 4.8 min; range 1–13 min) away from their nests without going to sea.

Trips commenced with one or more flights, lasting on average 9.1 ± 11.5 min (range 0.1–68 min). Return flights averaged shorter than outward flights (7.9 ± 7.6 min;

maximum 48.2 min), with birds apparently swimming ashore after three trips. There was a positive correlation between flight time at the start and end of each trip, but the relationship was weak ($r^2 = 0.268$, $n = 66$), and was not significant if the trip with the longest flying time was removed from the dataset ($r^2 = 0.027$). There were also frequent flights during foraging trips. Other studies of cormorant foraging behaviour have treated dives separated by flights as different bouts (e.g. Tremblay *et al.*, 2005), but Cape cormorants averaged 28 ± 24 (0–86) within-trip flights per trip, resulting in a median and mode of only one dive between flights (average 2.1 ± 2.8, maximum 44 successive dives). Most within-trip flights were brief (median 20 s, $n = 1886$), but there were some longer flights (maximum 60 min) and long rests between dives (maximum 114 min). Flights or rests > 5 min subdivided 14 trips into two to four bouts. For example, bird 4 left the colony at 07:25 h, flew for 33 min, landed and made two shallow dives, flew for a further 12 min and then landed for a protracted feeding bout comprising 85 dives interspersed by four brief flights (7–68 s). It then flew for a further 8 min, made 15 dives, followed by another 3-min flight and one dive, then made two long flights totalling 22 min and roosted on the water for 114 min. It then entered another phase of diving, with short 20–30-s flights between most dives, completing 46 dives and 39 flights in 61 min before finally flying for 8 min back to the colony.

Diving ecology

Dive data were obtained for 4186 dives (465 ± 151 dives per bird, range 256–699). The frequency distribution of maximum dive depths for all birds was unimodal, with an average dive depth of 10.2 ± 6.7 m (maximum 34 m) and dives lasting 21.2 ± 13.9 s (maximum 70 s). Four birds had bimodal dive distributions, and the modal depths of other birds ranged from < 5 to 10–15 m (Fig. 2). The average dive depths and durations among individuals ranged from 6.8 m and 14 s (bird 7) to 17.3 m and 44 s (bird 5), but there was less variability in the maximum dive depths (24–34 m) and the maximum dive durations (52–70 s). There was a strong relationship between dive duration and maximum depth (Table 1). Most dives (89%) exhibited some bottom time, with 40% of the dives having bottom times > 10 s (maximum 44 s). Bottom time increased with dive depth, but the relationship was weak compared with the total dive duration (Table 1). Vertical descent rate (average 1.42 ± 0.31 m s^{-1}) increased with dive depth (Table 1), suggesting steeper dive angles with increasing depth, but the effect was relatively weak, with little change in the rate beyond 10 m (Fig. 3). Ascent rates averaged slightly faster than descent rates (1.52 ± 0.41 m s^{-1}) and increased with the dive depth (Table 1).

There was considerable variation in the average dive depth within and among foraging bouts. The variability within bouts decreased with increasing mean dive depth (Fig. 4). Assuming that variable dive depths within bouts indicate pelagic diving (Grémillet *et al.*, 1998, 1999), this result suggests that deeper dives tend to be benthic, whereas
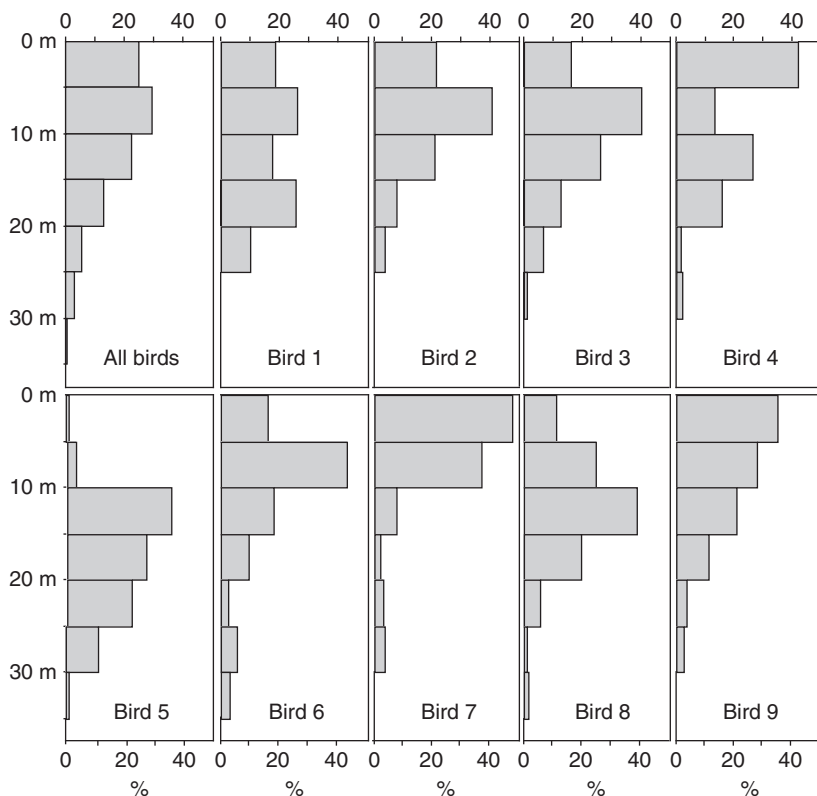
Figure 2 Frequency distributions (%) of maximum dive depths of nine breeding Cape cormorants *Phalacrocorax capensis*, and all birds combined.

Table 1 Correlations between dive duration, bottom time and descent and ascent rates with maximum dive depth (m)

	Slope	Intercept	r^2	n
Linear relationships				
Dive duration (s)	1.82	4.12	0.784	4186
Bottom time (s)[a]	0.649	3.99	0.256	3734
Descent rate (m s^{-1})	0.0230	1.15	0.213	3466
Ascent rate (m s^{-1})	0.0359	1.10	0.300	3414
Ln-transformed data				
Dive duration (s)	1.02	0.742	0.855	4186
Bottom time (s)[a]	0.761	0.357	0.294	3734
Descent rate (m s^{-1})	0.220	−0.181	0.284	3466
Ascent rate (m s^{-1})	0.295	−0.305	0.337	3414

[a]Excludes dives with no bottom time.
Ln-transformed data provide a better fit to the data, but linear regressions are also presented to facilitate comparison with other species.

pelagic dives tend to be shallower. This inference is supported by a higher proportion of IDZ dives at deeper depths (Fig. 5) and a negative correlation between dive depth CV and average dive depth within a bout ($r^2 = 0.372$, $n = 70$).
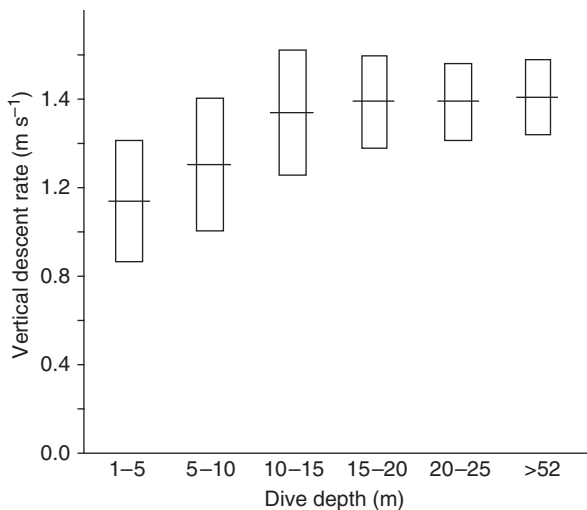
Recovery periods between dives typically were brief (mode 7 s, median 9 s, $n = 2236$) and were weakly correlated with the dive duration: post-dive rest (s) = $0.306 \times$ dive duration (s) + 5.96 ($r^2 = 0.219$). When birds took off after one or more dives, the rest periods were slightly longer than those between successive dives (mode 8 s, median 12 s,

$n = 1950$). However, the intervals between birds landing on the water and making their first dive averaged shorter (mode 4 s, median 6 s, $n = 1952$). Excluding rests > 60 s, the average duration of intervals between dives was 11.4 ± 7.6 s, with surface rests of 15.0 ± 11.0 s before flying and 7.4 ± 5.6 s after landing (excludes 1, 5 and 0.5% of records, respectively). By comparison, average rests between successive flights when no diving took place were much longer (median 78 s, 335 ± 869 s, $n = 131$).
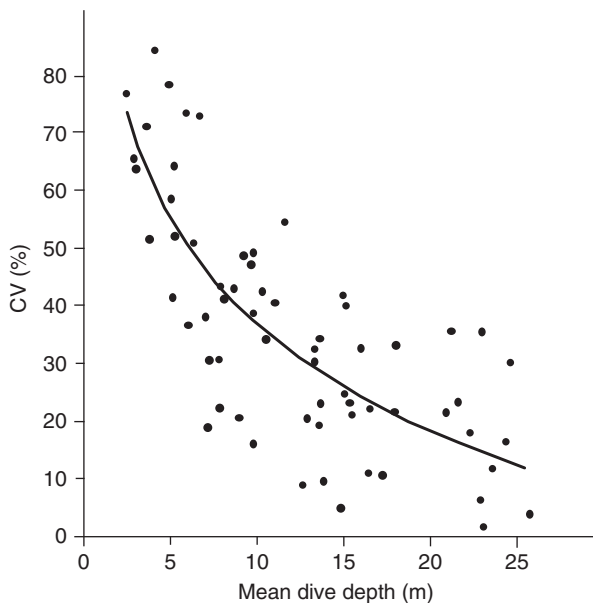
Diving efficiency (dive time:rest time) was 1.83 ± 1.31, with the average among bouts being 2.34 ± 1.13 (range 0.8–5.5, $n = 70$). Dive efficiency of a bout increased with the average dive depth: dive efficiency of a bout = $0.088 \times$ average dive depth (m) + 1.32 ($r^2 = 0.262$). Foraging efficiency averaged 0.30 ± 0.13 (maximum 0.69, $n = 1698$), decreasing for dives > 15 m deep (average efficiency was 0.30 for dives 1–5 and 5–10 m, 0.32 for 10–15 m, 0.29 for 15–20 m and 0.22 for dives to > 20 m; $F_{4,1690} = 5.99$, $P < 0.001$; only dives > 15 m significantly different from dives < 15 m; Tukey's test).

Activity budgets

Thirteen complete days of foraging were logged. Birds spent $5:30 \pm 1:34$ h (3:06–8:58 h) away from their nest, making 3.3 ± 1.0 foraging trips (2–5, $n = 13$) and 0.6 ± 0.8 trips within colonies (0–2) per day. There was a tendency for the second trip of the day to be the longest and have the most dives, but the differences between trips 1 ($n = 17$), 2 ($n = 16$),
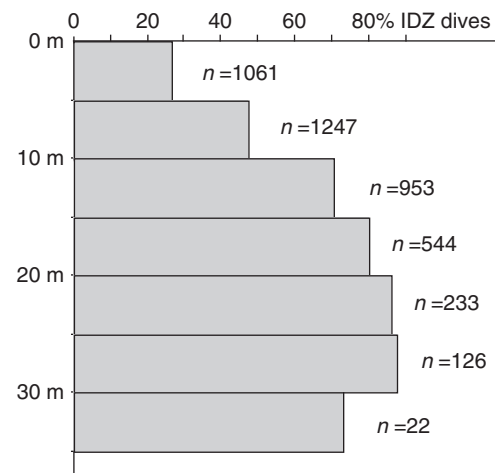
Figure 3 Change in descent rate (mean ± SD) as a function of dive depth in Cape cormorants *Phalacrocorax capensis.*

Figure 4 Variability in dive depth as a function of mean dive depth in Cape cormorant *Phalacrocorax capensis* foraging bouts ($r^2 = 0.604$).

Figure 5 Proportion of intra-depth zone (IDZ) dives as a function of maximum dive depth (*n* = number of dives).

Discussion

The dive durations of Cape cormorants were similar to those reported by direct observation: 19 ± 12 s Duffy (1989) and 24 s with rests of 8 s (Rand, 1960). Wilson & Wilson (1988) reported dives ranging from 20 to 75 s, with the dive duration increasing rapidly with water depth: dive duration (s) = $4.6 \times$ water depth (m) + 9.9. However, water depth was estimated in their study, and the regressions for all four species studied were steeper than reported in subsequent studies using data loggers to record dive profiles (Quintana *et al.*, 2007; Wilson *et al.*, 2008). Our results suggest that the dive durations of Cape cormorants increase more gradually in relation to dive depth, and are remarkably similar to other cormorants (excluding the imperial/blue-eyed complex; see Quintana *et al.*, 2007 for a review). Wilson & Wilson (1988) probably underestimated water depth for deep dives, resulting in their conservative estimate of the vertical dive rate ($1.0 \, \text{m s}^{-1}$). Our data show that Cape cormorants dive at $1.4 \, \text{m s}^{-1}$ (for dives > 10 m deep), similar to other cormorants (Ropert-Coudert, Grémillet & Kato, 2006).

Despite the accelerometer data suggesting that ascending was largely passive, ascent rates increased with dive depth (Table 1). Passive surfacing due to positive buoyancy should be faster in shallow water (Wilson *et al.*, 1992). However, two factors might increase their buoyancy when making deeper dives: they may inhale more air (Sato *et al.*, 2002; Wilson & Zimmer, 2004) or they may increase the amount of air in their plumage to improve insulation (Wilson & Wilson, 1995). Alternatively, birds making shallow dives may alter their body angle to reduce their ascent rate, especially when foraging for pelagic prey and not attempting to maximize bottom time.

The diving efficiency of Cape cormorants was similar to other cormorant species diving to relatively shallow depths (Cooper, 1986; Quintana *et al.*, 2007). Deep-diving cormorants have much lower diving efficiencies (< 1), presumably

3 ($n = 12$) and subsequent trips ($n = 11$) were not significant (ANOVA $F_{2,52} = 0.86$, $P = 0.47$ for trip duration and $F_{2,52} = 1.07$, $P = 0.33$ for number of dives). The total number of dives per day was 245 ± 91 (89–400), spending 88 ± 26 min (54–137 min) underwater. Birds spent 124 ± 53 min (44–243 min) on the water surface and 122 ± 51 min (45–222 min) flying, with 120 ± 36 (60–180) flights. The remainder of the day was spent ashore. Variance in daily flying time (CV = 41%) was higher than variance in diving time (CV = 30%), and similar to the variance in time spent resting on the water (CV = 43%).

as a result of anaerobic diving (e.g. Wanless, Harris & Morris, 1995; Tremblay *et al.*, 2005; Quintana *et al.*, 2007). The increase in dive efficiency with average dive depth is probably a consequence of short dive durations when making shallow dives. There may be limits on very short inter-dive periods other than constraints related to diving ability (e.g. interference by other birds when feeding in dense flocks). Foraging efficiency peaked for dives to 10–15 m. This contrasts with Crozet shags, whose foraging efficiency decreased gradually with increasing dive depth, albeit over a much greater depth range (Tremblay *et al.*, 2005). The foraging efficiency of Cape cormorants was only slightly less than that of Crozet shags when diving to > 10 m, but much less when making shallower dives (~ 0.3 vs. ~ 0.45; Tremblay *et al.*, 2005). This difference presumably also is a consequence of the high proportion of shallow dives targeting pelagic prey, where the dive profile is likely to be functionally different from dives where cormorants commute to benthic foraging areas.

Overall, the diving behaviour of Cape cormorants is similar to most other cormorants, despite their apparently greater buoyancy (Wilson *et al.*, 1992). Their total foraging time (5.5 h day^{-1}) is also similar to other cormorants provisioning small chicks, but their time spent diving per day was less (Table 2). Cape cormorants spent more time flying than all other species, and more time resting on the water than other shallow-diving cormorants. This latter factor resulted from protracted roosting at sea rather than long post-dive recovery periods. Long breaks in foraging trips might allow adults to digest prey for their own use and make space in the stomach for storing food for the chicks, analogous to the bimodal foraging pattern of Cape gannets (Ropert-Coudert *et al.*, 2004). The breaks might also allow birds to wait for a suitable foraging opportunity to arise. If aerial searching fails to locate any pelagic fish, it might pay to rest on the water to see whether other birds locate a school.

Flight in cormorants is expensive (Nelson, 2005), but several species utilize aerial searching to locate pelagic fish schools. This is best developed in Cape, guanay *Phalacrocorax bougainvillii* and Socotra cormorants *Phalacrocorax nigrogularis*, but is also practiced to a lesser extent by several other species (Nelson, 2005). In our study, Cape cormorants spent on average just over 2 h day^{-1} flying, with a maximum of almost 4 h. Variance in daily flying time was high (CV = 41%), probably because Cape cormorants exhibit multiple foraging strategies. Some foraging trips are 'typical' cormorant trips, with relatively short flights to foraging areas and a series of mainly benthic dives. By comparison, foraging trips targeting pelagic prey are likely to vary considerably in flying time, depending on how long it takes to encounter a school of fish. Once a school is located, foraging is characterized by a series of shallow dives interspersed by short flights as birds 'leap-frog' after the fleeing school (Rand, 1960).

Our study emphasizes the flexible foraging strategies exhibited by cormorants (Grémillet *et al.*, 1999, 2001, 2005). Other cormorants display a mix of pelagic and benthic foraging behaviour (e.g. Grémillet *et al.*, 1998; Ishikawa & Watanuki, 2002), but Cape cormorants are extreme in the distance they travel in search of pelagic prey, and in resting on the water between foraging bouts to avoid commuting to land. Studies of guanay and Socotra cormorants will probably reveal similar activity budgets to Cape cormorants. There are few data on these species, but their dive durations are similar (Cooper, 1986), and the duration of foraging trips by non-breeding guanay cormorants is highly variable, indicative of an unpredictable, patchy prey resource (Zavalaga & Paredes, 1999).

Compared with the other main seabird predators of pelagic fish in the Benguela upwelling region, Cape cormorants made shorter, more frequent foraging trips. Cape gannets and African penguins typically have foraging trips lasting 1–2 days (Wilson, 1985; Ropert-Coudert *et al.*, 2004; Petersen *et al.*, 2006). The foraging range of Cape cormorants while feeding small chicks is *c*. 7 ± 6 km (maximum 40 km, $n = 66$ trips), similar to penguins (10–20 km, Petersen *et al.*, 2006), but appreciably less than gannets (50–200 km, Grémillet *et al.*, 2004; Pichegru *et al.*, 2007). Successful breeding by large colonies of cormorants probably depends on the reliable occurrence of pelagic fish schools within this foraging range (Crawford & Dyer, 1995). As a result, no-fishing zones within 20 km of breeding colonies designed to ensure adequate fish for breeding African penguins should also benefit Cape cormorants.

Table 2 Daily activity budgets (min) of Cape Cormorants *Phalacrocorax capensis* compared with other cormorants expressed as the total time as well as a proportion of local day length (civil dawn to dusk)

Species	Diving	Rest on water	Flying
Cape cormorant *Phalacrocorax capensis*	88 ± 26 (10%)	124 ± 53 (14%)	122 ± 51 (14%)
European shag *Phalacrocorax aristotelis*[a]	129 ± 56 (12%)	118 ± 17 (11%)	53 ± 11 (5%)
Rock shag *Phalacrocorax magellanicus*[b]	246 ± 45 (26%)	71 ± 22 (7%)	29 ± 6 (3%)
South Georgia shag *Phalacrocorax georgianus*[c]	125 ± 32 (13%)	218 ± 49 (23%)	22 ± 7 (2%)
Crozet shag *Phalacrocorax melanogenis*[d]	159 ± 46 (17%)	176 ± 37 (19%)	23 ± 6 (2%)

Data from
[a]Wanless & Harris (1992);
[b]Quintana (2001);
[c]Wanless *et al.* (1995);
[d]Tremblay *et al.* (2005).
All birds were provisioning small chicks.

Acknowledgements

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