Seabird predation by white shark *Carcharodon carcharias* and Cape fur seal *Arctocephalus pusillus pusillus* at Dyer Island

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Both the white shark (*Carcharodon carcharias)* and Cape fur seal (*Arctocephalus pusillus pusillus)* prey on and/or attack seabirds in South Africa. The Dyer Island region abounds in these predators, as well as seabirds, including the African penguin (*Spheniscus demersus*), Cape cormorant (*Phalacrocorax capensis*), bank cormorant (*P. neglectus*), white-breasted cormorant (*P. carbo*), and crowned cormorant (*P. coronatus*). Between August 1999 and February 2001, predatory interactions among these taxa were quantified and qualified by the routine collection and inspection of seabird carcasses and injured birds, as well as opportunistic observations of live attacks. White sharks are infrequent predators of seabirds at Dyer Island, perhaps due to an abundance of Cape fur seals (a preferred prey), anti-predator behaviour by penguins, and seabirds not being a preferred prey type. Cape fur seals were more conspicuous seabird predators, each year attacking adult penguins (1.99–2.52%), white-breasted cormorants (5.21–5.72%), and crowned cormorants (3.13%), as well as a single bank cormorant. Cape fur seals killed an estimated 0.83–1.09% of the fledgling Cape cormorants. Attacks on penguins at the island are crepuscular as birds depart to and return from foraging grounds. Fledgling Cape cormorants are frequently attacked when alighting on water following disturbance and failed flight attempts, or for bathing. Human disturbance, which may force birds to take to the water, may cause inter-annual differences in the predation impact on this taxon.

Key words: African penguin, Cape fur seal, cormorants, Dyer Island, predation, white shark.

INTRODUCTION

Many South African seabird populations are declining due to various threats (Barnes 2000). Both human-induced factors such as oil pollution, egg harvesting, human disturbance (Hockey & Hallinan 1981; Shelton *et al.* 1984; Crawford *et al.* 2000) and natural effects, including predation, interspecific competition for nesting sites, modification to fish stocks (Crawford *et al.* 1989, 1990; Crawford & Dyer 1995; Marks *et al.* 1997; David *et al.* 2003) have been implicated as possible contributors to seabird declines. Quantitative accounts of seabird predation are rare (*e.g.* Du Toit *et al.* 2004), and therefore the relative importance of predatory attacks in population declines is currently unknown.

A number of apex predators attack, feed on or induce anti-predator behaviour in seabirds in southern Africa including the Cape fur seal (Shaughnessy 1978; Broni 1985; Marks *et al.* 1997; David *et al.* 2003), the white shark (Randall *et al.* 1988) and the killer whale (*Orcinus orca*) (Randall & Randall 1990). The Cape fur seal is a most conspicuous seabird predator and has been recorded hunting and feeding on gannets, *Morus capensis* (Du Toit 2002; David *et al.* 2003), cormorants, *Phalacrocorax* spp. (Marks *et al.* 1997) and penguins (Shaughnessy 1978; Crawford *et al.* 2001; Du Toit 2002). Up to 7.1% of the fledgling population of Cape cormorants at Dyer Island may fall victim to seals annually (Marks *et al.* 1997), while Du Toit (2002) estimated that 0.9% of the African penguin population on Ichaboe Island, Namibia, succumbed to seal predation. David *et al.* (2003) calculated that 7.4% of the fledgling Cape gannet population at Malgas Island, South Africa, was killed by Cape fur seals during the

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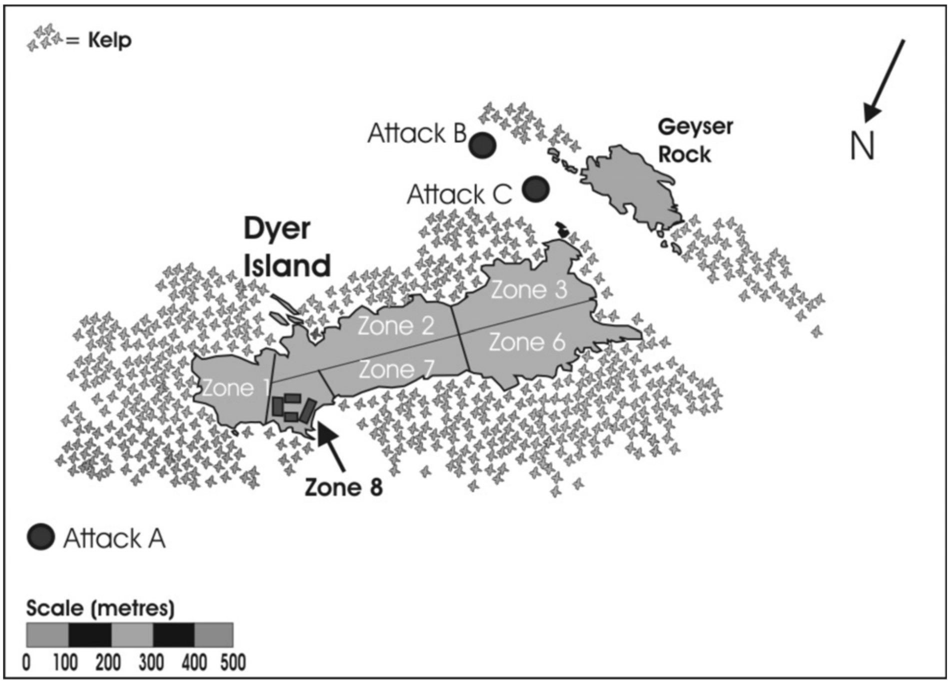

Fig. 1. Map of the Dyer Island study site with zonation illustrated. Also indicated is the location of three attempted attacks by white sharks on kelp gulls.

November 2000 – March 2001 breeding season. These estimates are large enough to warrant more attention to such attacks.

Southern Africa is one of the centres of abundance for the white shark (Compagno 1991) where it ranges from southern Mozambique to Namibia. White sharks were responsible for a majority of the injured and dead African penguins recovered from the shoreline of St Croix Island and Bird Island, Algoa Bay, South Africa (Randall *et al.* 1988). However, only a single African penguin has been recovered from a white shark stomach (Bass *et al.* 1975).

Resident birds on Dyer Island identified as vulnerable to attack by either the Cape fur seal or white shark include the African penguin (Shaughnessy 1978; Randall *et al.* 1988) and the four cormorant species (Marks *et al.* 1997; Du Toit 2002; David *et. al.* 2003; Crawford 2005a–d). The African penguin is the only endemic penguin in southern Africa, and is listed as 'Vulnerable' by the World Conservation Union (IUCN) due to a persistent population decline (Crawford *et al.* 1990; Barnes 2000). The IUCN further classifies the endemic crowned cormorant as 'Near-threatened' because of its small population size (Barnes 2000). The endemic bank cormorant is currently classed as 'Endangered' due to ongoing population declines (Crawford 2005c). The Cape cormorant is classed as 'Near-threatened' due to a population decrease from 277 000 pairs to *c.* 72 000 pairs between 1977 and 1996 (Barnes 2000). The white-breasted cormorant is not threatened in South Africa (Barnes 2000).

Most research efforts have been directed at single predator-prey interactions, despite the need for ecosystem based management (David *et. al.* 2003). The diversity and abundance of predator and prey species occurring within the Dyer Island area enable an unprecedented array of interspecific predatory interactions to be documented and investigated. The aim of this paper is to determine the comparative importance of seabird predation by white sharks and Cape fur seals on the resident seabird populations at Dyer Island.

STUDY AREA

The Dyer Island complex (34°41′S; 19°25′E) lies off the Western Cape Province of South Africa, and consists of two islands (Fig. 1). Dyer Island is the largest with a surface area of 20 ha and is extensively inhabited by seabirds; Geyser Rock is the smaller island, lying 230 m southwest of Dyer Island. Geyser Rock is host to an estimated 55 000

Cape fur seals (J.H.M. David, pers. comm.). Dyer Island was subdivided into six zones to facilitate the present study (Fig. 1) as outlined below.

METHODS AND MATERIALS

Predatory encounters were investigated through opportunistic observation of attacks, collection of bird carcasses and observation and/or collection of injured seabirds between August 1999 and February 2001. Daily searches for injured birds and washed-up seabird carcasses in the intertidal zone were carried out during a circumperambulation of Dyer Island. All seabird carcasses discovered were removed, examined and buried. The taxa (species level), date, location (zone), age class, sex (for sexually dimorphic species only) and stage of decomposition (fresh vs skeletal remains) were recorded postmortem. Where applicable, injuries on the carcasses were described, and when possible the predator identified. Depending on the severity of the injury, and the degree of disturbance the collection of data would cause, injured seabirds were both collected for examination and treated, or simply examined in the field and released. During examination the wound characteristics were described, and when possible the predator identified. Each victim's location (zone), age-class, sex and the wound severity (superficial, serious, mortal) were routinely recorded.

Live attacks were observed opportunistically from various vantage points, including an observation tower (height 4 m), within the living compound, during daily circum-island research patrols, and from a research vessel anchored at various locations in the near vicinity of the island (Fig. 1). Predation cues included: splashing; hovering kelp gulls (*Larus dominicanus*); a splashing seal, or the formation of an oil slick as a result of natural internal oils emanating from a disembowelled seabird. The predator and prey species involved (cormorants to genus level only) were recorded, together with the time, location of the event, local environmental conditions, and a description of the encounter.

Moulting and breeding population trends in the African penguin and four cormorant species were established by fortnightly counts of moulting penguins, and a monthly nest count of all birds (Crawford & Boonstra 1993). A total of 34 counts of moulting African penguins were completed between August 1999 and January 2001. Moult counts (adults only) conducted between November 1999 and October 2000, December 1999 and November 2000, and January 2000 to December 2000 were summed independently and averaged to estimate the breeding population size on Dyer Island conservatively. Monthly nest counts of all occupied cormorant nests, defined as sites defended by adult birds or sites with eggs or chicks, were carried out. Peak nest counts of the Cape, bank, crowned and white-breasted cormorant species were multiplied by two (breeding pairs) to estimate the numbers of cormorants at Dyer Island conservatively.

The predatory impact of Cape fur seals on the African penguin population was taken as the percentage of the adult population (established by moult counts) killed between January 2000 and December 2000. The fledgling population of Cape cormorants was calculated by multiplying the peak nest count by 2.36 (average eggs/nest) (Crawford 1992). The survival coefficients between eggs and chicks (0.87) and chicks to fledglings (0.91) were then used to establish the fledgling population (Crawford 2005d). The annual impact of predators on other cormorant species was taken as the percentage of the population (established by peak nest count) killed during the corresponding 12 months (January–December 2000). For each analysis, the lower minimum estimate includes only carcasses of birds definitely killed by Cape fur seals, while the upper minimum includes skeletal remains that could have come from seabirds killed by fur seals. Both estimates are conservative, as unknown proportions of carcasses do not wash up on Dyer Island. Diel and seasonal trends in attack frequency were tested using analysis of frequency tests (χ^2 test), with significance set at the 5% level.

RESULTS

Seabird carcasses

Between August 1999 and January 2001 a total of 812 seabird carcasses were collected (Table 1). Of these the African penguin, Cape cormorant, bank cormorant, crowned cormorant, white-breasted cormorant and Cape gannet showed evidence of predation. Predation by Cape fur seals evidently caused the death of 71.6% of the birds, while no carcasses displayed evidence of a white shark bite. Approximately 7.5% of the carcasses showed no evidence of predation, while advanced decomposition prevented the establishment of the cause of death in the remaining 20.9% of carcasses. Some 87.7% of the corpses that displayed

Table 1. Cause of death in the various species of seabird carcasses collected from the intertidal region of Dyer Island between September 1999 and January 2001.

Species	Cause unknown	No. injuries apparent	C.F.S. wounds present	W.S. wounds present	Total no. of carcasses
African penguin	45 (21.0%)	15 (07.0%)	154 (72.0%)	0 (00.0%)	214
Cape cormorant	115 (17.4%)	42 (11.3%)	396 (71.6%)	0 (00.0%)	553
Bank cormorant	0 (00.0%)	0 (00.0%)	1 (100%)	0 (00.0%)	1
Crowned cormorant	1 (07.7%)	3 (23.1%)	9 (69.2%)	0 (00.0%)	13
White-breasted cormorant	3 (12.5%)	1 (04.2%)	20 (83.3%)	0 (00.0%)	24
Gannet	0 (00.0%)	0 (00.0%)	1 (100%)	0 (00.0%)	1
Cormorant sp.	6 (100%)	0 (00.0%)	0 (00.0%)	0 (00.0%)	6

C.F.S. = Cape fur seal, W.S. = white shark.

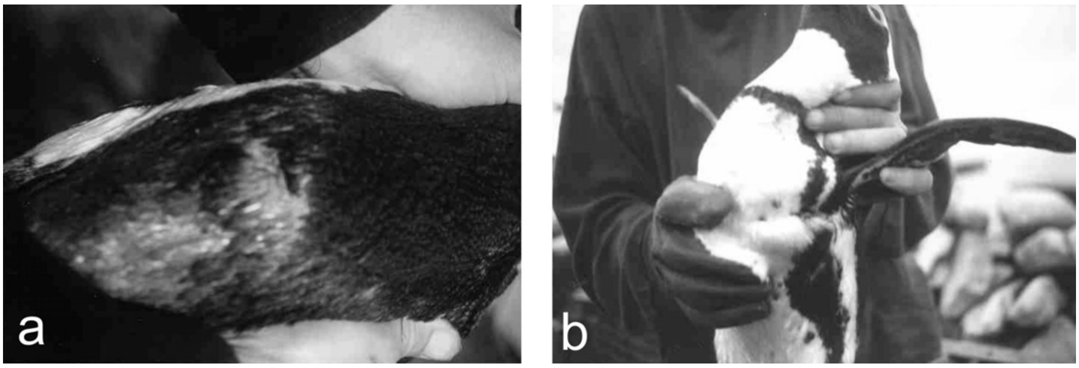

Fig. 2. White shark-inflicted wounds on African penguins; **a**, a single elongated puncture is visible on the dorsal surface; **b**, multiple punctures to the body cavity characterize this bite.

Cape fur seal inflicted wounds were 'degloved' as defined by Marks *et al.* (1997). Abdomen and neck bites accounted for the remaining 5.2% and 7.1% of injury to carcasses, respectively.

Injured seabirds

Injured seabirds included the African penguin and Cape cormorant. Excluding birds contaminated by oil, 26 of 31 birds were African penguins, while the remainder were Cape cormorants. Predation was adjudged the cause of injury in only 10 birds, with three Cape cormorants and five penguins sporting wounds inflicted by Cape fur seals. Two penguins showed evidence of white shark bites, the only evidence of white sharks attacking African penguins in this study (Fig. 2a,b).

Live attacks

A total of 204 attacks by Cape fur seals on African penguins and cormorant spp. were observed. Of these 46.6% involved the African penguin, 38.7% a cormorant sp., and in the remaining 14.7% of attacks the victim was not identified (Table 2). Additionally, three encounters between white sharks and kelp gulls were observed (Table 2). White sharks attacked floating gulls twice within the channel area, adjacent to Geyser Rock (attacks B and C, Fig. 1). During attack 'B' the white shark successfully hit, and killed, the gull

Table 2. Live attacks by various predators on seabirds occurring at Dyer Island. 'Unsuccessful attempt' represents all occasions when predator(s) made an unambiguous attempt to attack potential prey but failed.

	White shark	Cape fur seal
Successful attacks		
African penguin	0	92
Cormorant sp.	0	79
Kelp gull	1	0
Unknown	0	32
Unsuccessful attacks		
African penguin	0	0
Cormorant sp.	0	1
Kelp gull	2	0
Unknown	0	0

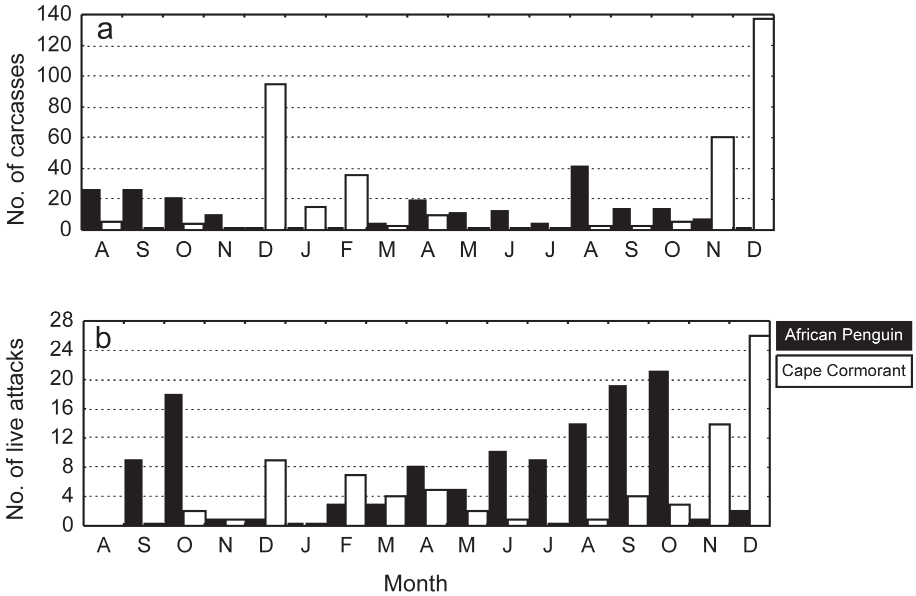

Fig. 3. Seasonal trends in seabird predation at Dyer Island; **a**, collected seabird carcasses; **b**, observed attacks by Cape fur seals.

but did not return to feed on it. The third encounter (attack A) was a breach from a white shark of *c.* 380 cm total length towards two hovering gulls that failed to make contact.

Seasonal trends in Cape fur seal attacks

Attacks on African penguins by Cape fur seals were seasonal, with few penguin carcasses collected during the early (October to December) and late (January to March) summer periods ($\chi^2_{(0.05,3)}$ = 44.2, $P < 0.01$) (Fig. 3a). Predation on Cape cormorants by Cape fur seals showed a significant seasonal pattern ($\chi^2_{(0.05,3)}$ = 232.3, $P < 0.001$) with large numbers of carcasses collected in the early and late summer periods in both 1999 and 2000 (Fig. 3a). White-breasted cormorant carcasses appeared aseasonally ($\chi^2_{(0.05,3)}$ = 1.87, $P > 0.50$) (Fig. 4a). The recovery of crowned cormo-

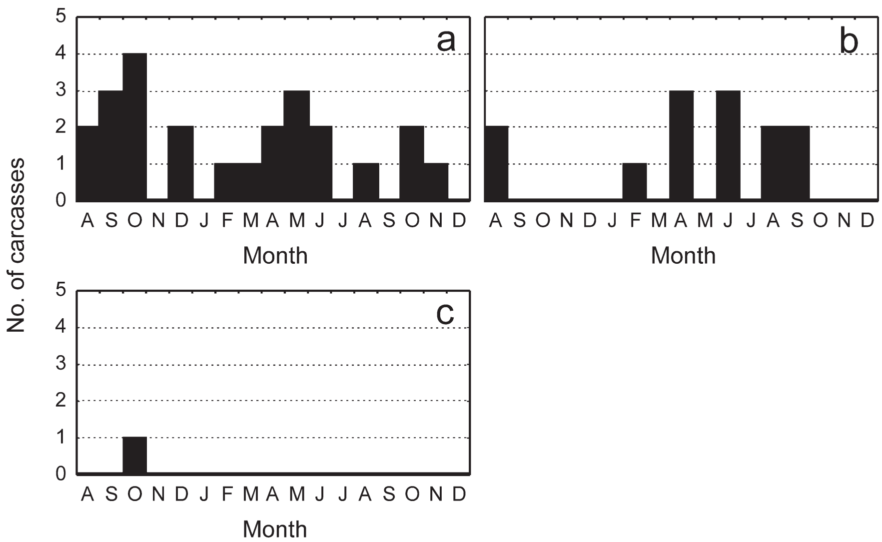

Fig. 4. Seasonal patterns of carcass collection for three species of cormorants resident on Dyer Island; **a**, white-breasted cormorant; **b**, crowned cormorant; **c**, bank cormorant.

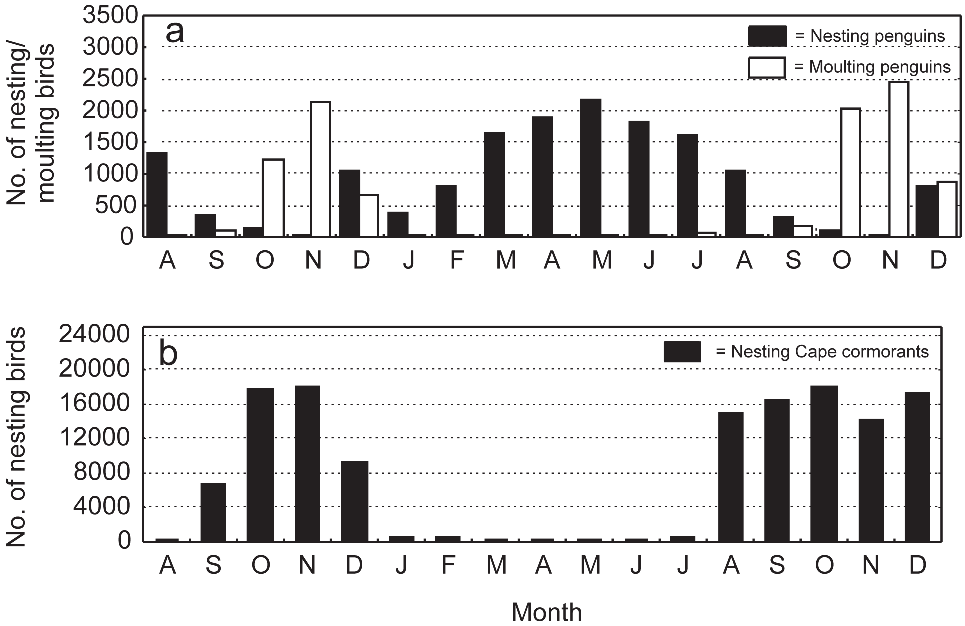

Fig. 5. Nesting and moulting trends of seabirds at Dyer Island; **a**, African penguins; **b**, Cape cormorants.

rant carcasses was seasonal ($\chi^2_{(0.05,3)}$ = 8.4, P < 0.05) with 92% of the carcasses collected in the early (April to June) and late (July to September) winter period (Fig. 4b). Only one carcass of a bank cormorant was recovered in October 1999 (Fig. 4c). The seasonal trends in attacks by Cape fur seals on seabirds mimicked trends of carcass recovery (Fig. 3b). Live attacks on African penguins were seasonal, with few attacks seen during the late summer period ($\chi^2_{(0.05,3)}$ = 23.3, P < 0.001). The majority of the attacks observed involving cormorant spp. occurred in early summer ($\chi^2_{(0.05,3)}$ = 27.3, P < 0.001) (Fig. 3b).

Population trends of seabirds

The African penguin is a seasonal breeder at Dyer Island, with peak nest counts recorded between March and August (Fig. 5a), while the peak moulting period is between October and December (Fig. 5a). Nest counts of Cape cormorants showed that in 1999 nesting began in earnest during September, while in 2000 it began slightly earlier in August (Fig. 5b).

Diurnal trends in Cape fur seal attacks

Significant diurnal trends in the minimum rate of live attacks existed for both penguins ($\chi^2_{(0.005,13)}$ = 71.13, P < 0.01) and cormorants ($\chi^2_{(0.005,13)}$ = 24.21, P < 0.05) (Fig. 6). Differences existed in the diurnal patterns of attack on penguin and cormorants (2 × 14 contingency table, $\chi^2_{(0.005,13)}$ = 45.25, P < 0.01). Crepuscular peaks in penguin attacks were evident, while attacks on cormorants increased throughout the morning period, and peaked at around 13:00, before trailing off (Fig. 6b).

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Importance of predation in seabird mortality

The African penguin breeding population was estimated at 5081 birds. During the corresponding 12 months (Jan 2000 – Dec 2000) a total of 134 penguin carcasses were collected of which 101 showed evidence of Cape fur seal attack. The remaining 33 birds were either too decomposed for cause of death to be established (27 birds), or no injuries were apparent (six birds). Therefore, a lower minimum of 1.99% (and an upper minimum of 2.52%) of the breeding population died from Cape fur seal attacks during this period. White-breasted cormorants were the most vulnerable cormorant species to seal attack, which resulted in

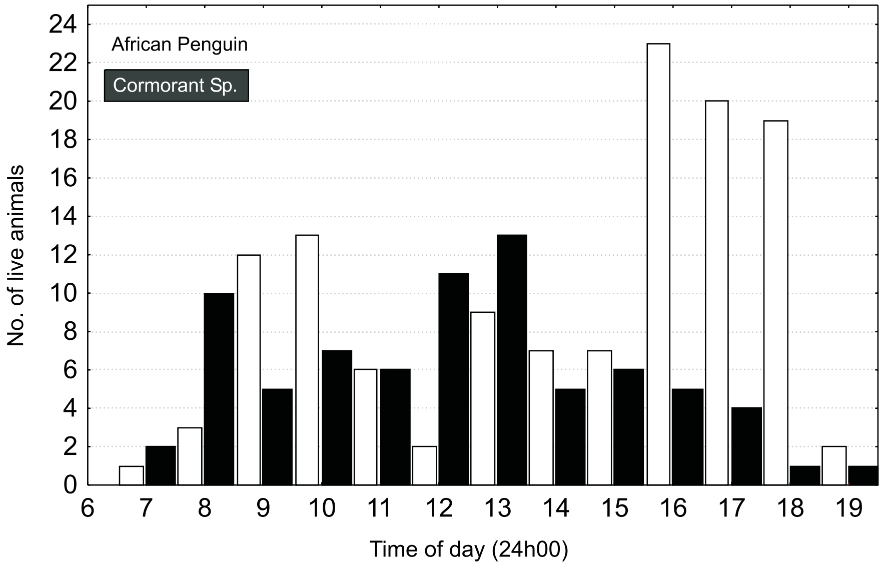

Fig. 6. Diel patterns in live attacks on seabirds at Dyer Island.

Table 3. Predatory impact of Cape fur seals on cormorant spp. at Dyer Island between January 2000 and December 2000.

Species	Peak nest count	Population estimate	Seal predation	Annual predation impact (%)
Bank cormorant	42	84	Min: 0	0.00
			Max: 0	0.00
Crowned cormorant	128	256	Min: 8	3.13
			Max: 8	3.13
White-breasted cormorant	96	192	Min: 10	5.21
			Max: 11	5.72

the death of at least 5.72% of the population (Table 3). Crowned cormorants (3.13%) appear less affected and bank cormorants virtually unaffected (Table 3). The peak nest count of Cape cormorants (18 105) translates to a fledgling population of 33 827 fledglings during the 2000/2001-year. A lower minimum of 280 and an upper minimum of 370 fledgling Cape cormorants were killed by Cape fur seals during the corresponding period (Janoury 2000 – December 2000). This suggests an annual minimum predation rate of between 0.83% and 1.09% of the fledgling population.

DISCUSSION

White sharks do not appear to be a major threat to seabirds at Dyer Island, in contrast to the situation at St Croix Island, despite similar methods of observation used to investigate the trends in attacks on seabirds (Randall *et al.* 1988). The most conspicuous difference between the two ecosystems is the presence of a large Cape fur seal colony at Dyer Island, but not at at St Croix Island. This may have a number of direct and indirect effects on the behaviour of penguins and white sharks.

Pinnipeds represent a primary prey for white sharks (Le Boeuf 1982; Klimley *et al.* 1992; Compagno *et al.* 1997). The *c.* 55 000 strong seal colony may direct the attention of white sharks towards this prey, and consequently, less effort may be spent investigating alternative prey that is not as energetically rewarding, or not part of their typical diet (Bass *et al.* 1975; Cliff *et al.* 1989, 1996). Anti-predator behaviour (fleeing to and from an island) of African penguins in the vicinity of pinnipeds, and other predators, has been well documented (Randall & Randall 1990), and was frequently observed at Dyer Island (this study). Such behaviour would also make penguins less vulnerable to investigatory bites from white sharks.

Injured survivors offered the only evidence of white sharks attacking penguins. The relatively gentle nature of these bites suggests curiosity or inspection as possible motivation, rather than feeding. This is consistent with the wide diversity of non-prey items that have been bitten by white sharks (Collier *et al.* 1996), as well as, infrequent consumption of non-prey species such as humans (*Homo sapiens*) (Burgess & Callahan 1996), sea otters (*Enhydra lutris*) (Ames & Morejohn 1980) and African penguins (Bass *et al.* 1975) following an attack.

Penguins were attacked by Cape fur seals seasonally with lowest attacks during November and December, the peak moulting period of the penguins. Penguins remain on land during their moult, except for preening and drinking (Cooper 1974) and restrict foraging to a minimum (Broni 1985). Penguins at Dyer Island appear to be most vulnerable to seal predation during foraging related movements away from, and subsequent return to, the island. The crepuscular pattern of such live attacks (this study) coincides with the mean departure (08:00) and arrival time (17:30) of foraging penguins during the breeding season at Marcus Island, Western Cape (Wilson *et al.* 1988). Cape fur seals take at least 1.99% to 2.52% of the adult breeding population of penguins at Dyer Island, an underestimate as only some carcasses end up on Dyer Island's shore. In addition, the loss of a breeding adult results in the loss of its clutch, thus further compounding the predation impact.

Cape cormorants appear vulnerable to predation by seals due to their frequent landing in the waters surrounding Dyer Island. The presence of cormorants in the inshore area of Dyer Island is not necessarily related to feeding, as feeding occur up to 40 km from shore (Berry 1976) in sub-surface waters (Crawford 2005d). The alighting of cormorants on waters close to shore followed failed flight attempts and/or onshore disturbance (this study) and the seasonal peak in attacks corresponded to the annual fledging periods of this species. The period between egg laying and fledging is from 10 to 12 weeks (Crawford 2005d), and in both 1999 and 2000, attacks on fledgling Cape cormorants concomitantly rose sharply three months after nesting began. Cape cormorants tended to be attacked throughout the day, with a peak around midday. Disturbance, failed flight attempts and bathing often resulted in large numbers of fledgling cormorants swimming in the waters adjacent to Dyer Island. In particular when approach from humans causes a chain reaction of panic, masses of fledglings flee to the water. The conservative estimate that 1.09% of the Cape cormorant fledgling population succumb to seal predation is noticeably lower than the 7.1% calculated by Marks *et al.* (1997) for Dyer Island. One factor that may have contributed to the large difference was the level of human disturbance experienced by the respective fledgling populations. Extensive observation periods, from a tower constructed on the southwestern point of Dyer Island, were necessary for land based observations of the channel area during the study of Marks *et al.* (1997). This may have contributed to more fledglings entering the water due to human disturbance by observers moving to and from the tower, and movement on the tower, than during the present study.

It can be concluded that the continual decrease in penguin numbers in South Africa requires management to attempt to minimize all factors contributing to the decline, including seal predation (David *et al.* 2003). Active removal of rogue seals at Malgas Island saw significant declines in attack rates in 1999 and 2000 (David *et al.* 2003). Disturbance, human or otherwise, of penguins on the island does not appear to play a major role in increasing seal predation rate, as most penguins are attacked when travelling to and from their feeding grounds. This quantitative account of Cape fur seals attacking and consuming bank, crowned and white-breasted cormorants in southern Africa shows that these attacks are comparatively infrequent and opportunistic. However, the impact on the small local cormorant populations is significant due to their low abundance and vulnerability to stochastic disturbances. Human disturbance in particular, should be minimized in areas and at times when cormorants are breeding and fledglings are present.

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